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Modeling sources of variation for growth and predatory demand of Lake Erie walleye (*Stizostedion vitreum*), 1986–1995

Mark W. Kershner, Denise M. Schael, Roger L. Knight, Roy A. Stein, and Elizabeth A. Marschall

Abstract: Given the variable nature of the Lake Erie ecosystem, we investigated biotic and abiotic sources of variation for walleye (*Stizostedion vitreum*) growth, consumption, and population-wide predatory demand. We determined how temperature, population structure, and age-specific consumption influenced walleye growth and consumption during 1986–1995. For each year, we used individual-based bioenergetics modeling to compare growth and consumption by walleye in Lake Erie's western or central basin with those of walleye moving seasonally between basins. Population structure strongly affected walleye growth and consumption but had little influence on interbasin growth rate comparisons. Based on water temperature alone, growth and consumption by western basin walleye were generally lower than for central basin or migratory populations and were more limited by summer water temperatures. In simulations combining effects of population structure, temperature, and age-specific consumption, migratory walleye grew most rapidly, taking advantage of temperature-related growth peaks in both basins. Estimates of walleye predatory demand declined with population size from 1988 through 1995. With natural feedbacks, predatory demand interacts with prey production, limiting walleye reproductive potential when prey availability is low. However, immediate impact on predatory inertia is limited, complicating our ability to predict how predatory demand and prey availability interact in Lake Erie.

Résumé : Étant donné la nature variable de l'écosystème du lac Érié, nous avons examiné les sources biotiques et abiotiques de variation de la croissance, de la consommation et de la demande de prédation à l'échelle de la population chez le doré jaune (*Stizostedion vitreum*). Nous avons déterminé en quoi la température, la structure de la population et la consommation spécifique à l'âge influaient sur la croissance et la consommation des dorés entre 1986 et 1995. Pour chaque année, nous avons eu recours à la modélisation bioénergétique individuelle pour comparer la croissance et la consommation chez les dorés du bassin du centre ou de l'ouest du lac Érié et chez des dorés qui se déplacent de façon saisonnière entre les bassins. La structure des populations affectait fortement la croissance et la consommation des dorés jaunes, mais avait peu d'influence sur les comparaisons des taux de croissance entre bassins. Si l'on se fondait seulement sur la température, la croissance et la consommation chez les dorés jaunes du bassin occidental étaient dans l'ensemble inférieures à celles des dorés du bassin central ou des populations migratrices, et étaient plus limitées par les hautes températures estivales. Dans des simulations combinant les effets de la structure démographique, de la température et de la consommation spécifique à l'âge, les dorés migrateurs se développaient plus vite car ils tiraient profit des pics de croissance liés à la température dans les deux bassins. Les estimations de la demande de prédation des dorés ont baissé avec l'effectif de la population entre 1988 et 1995. Avec les rétroactions naturelles, la demande de prédation interagit avec la production de proies, limitant le potentiel génésique des dorés quand la disponibilité des proies est faible. Toutefois, l'impact immédiat sur l'inertie du comportement de prédation est limité, ce qui complique notre capacité de prédire le mode d'interaction entre la demande de prédation et la disponibilité des proies dans le lac Érié.

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Introduction

Understanding the dynamic nature of carrying capacity is critically important to fisheries managers and aquatic ecologists, whose goals include assessment and understanding of factors affecting recruitment and survival of individual fish species. In many systems (e.g., the Great Lakes: Stewart et al. 1981; Stewart and Ibarra 1991; Jones et al. 1993), efforts focus on the balance between prey availability and predatory demand, as this relationship can determine the biomass and abundance of large piscivores (Carpenter et al. 1985). For example, in Lake Erie, concern has been raised regarding the capacity of the extant prey fish assemblage to support Lake Erie's walleye (*Stizostedion vitreum*) population, particularly during periods of shifting lake productivity.

In fact, biotic and abiotic characteristics of the Lake Erie ecosystem have changed substantially during the past 25–30 years (e.g., Makarewicz and Bertram 1991). With declines in lakewide phosphorus loading and a commensurate increase in water clarity, Lake Erie's trophic status has been rapidly shifting from eutrophy to mesotrophy in its western basin and from mesotrophy to oligotrophy in its central and eastern basins. During this time, western and central basin prey fish assemblages have experienced shifts in relative abundance among three prey types: (*i*) spiny-rayed fishes (yellow perch (*Perca flavescens*), white perch (*Morone americana*), white bass (*Morone chrysops*), freshwater drum (*Aplodinotus grunniens*)), (*ii*) soft-rayed fishes (emerald shiner (*Notropis atherinoides*), spottail shiner (*Notropis hudsonius*), rainbow smelt (*Osmerus mordax*), trout-perch (*Percopsis omiscomaycus*)), and (*iii*) clupeids (gizzard shad (*Dorosoma cepedianum*), alewife (*Alosa pseudoharengus*)) (Knight and Vondracek 1993). These fluctuations within the prey assemblage are likely influenced by shifts in abiotic factors (e.g., lake trophic status, nutrient availability, and winter severity) and walleye predatory demand (Knight et al. 1984; Francis 1992; Hartman and Margraf 1992; Knight and Vondracek 1993). Walleye predatory demand, in turn, has been influenced by dramatic increases and fluctuations in walleye population size from 1970 to the present (Hatch et al. 1987; Knight 1997). Lake Erie also has endured numerous successful species invasions (e.g., zebra mussels (*Dreissenia polymorpha*), quagga mussels (*Dreissena bugensis*), white perch, round goby (*Neogobius melanostomus*), and a zooplankter, *Bythotrephes cederstroemi*) (Mills et al. 1993). More generally, variability of complex biotic and abiotic interactions in Lake Erie will determine the lake's carrying capacity for its top predator and associated prey assemblage. With this level of biotic and abiotic flux, the Lake Erie ecosystem represents a substantive challenge for fisheries managers and ecologists, who must balance short-term resource management goals (regarding walleye and their prey) with long-term resource sustainability, seeking what can only be described as a fix on a "moving target."

Given this variable ecosystem, we sought to gain insight into the influence of biotic and abiotic factors on variability associated with predatory demand in Lake Erie by modeling patterns of consumption and growth for walleye, the top predator. Lake Erie walleye differ from top predators in other Great Lakes in that they are naturally reproducing rather than stocked. Thus, natural feedback mechanisms may be in place to mediate walleye population dynamics. For example, Hartman and Margraf (1992) suggested that Lake Erie walleye growth was influenced by effects of walleye abundance on the prey fish assemblage. Growth and energetic condition of Lake Erie's walleye spawning stock and subsequent year-class strength appear to be strongly related (Henderson and Nepszy 1994), with fall gizzard shad (lipid-rich prey fish preferred by walleye) abundance strongly affecting walleye spawning success in the following spring (Madenjian et al. 1996). These results indicate the existence of a strong natural feedback mechanism between walleye growth and reproductive success.

Herein, we examine the relative importance of temperature regime and walleye age and size structure to patterns of walleye growth and consumption during 1986–1995. We incorporated walleye abundance and population structure, historically variable in Lake Erie, to account for "predatory inertia," a situation where increased predator abundance and (or) growth lead to increased predator biomass and predatory demand (Stewart et al. 1981; Carpenter et al. 1985). In addition, given evidence for seasonal walleye migration among Lake Erie's three basins (which differ in temperature regime and prey availability) and Lakes St. Clair and Huron (M. Turner (Ohio Department of Natural Resources, Division of Wildlife (ODNR-ODW), R. Haas (Michigan Department of Natural Resources), and S. Nepszy (Ontario Ministry of Natural Resources), unpublished tagging data), we explored the energetic consequences of seasonal migration by walleye.

To accomplish these goals, we used an individual-based bioenergetics model (Kitchell et al. 1977; Hewett and Johnson 1992) parameterized for walleye resident in Lake Erie's western and central basins during 1986–1995. For a given growing season, we modeled independent and combined effects of basin-specific temperature regimes, walleye age and size structure, and daily consumption rates to determine their effects on growth and consumption by walleye resident in either the western or central basin or walleye moving seasonally between them. Finally, to provide insight into the balance between predatory demand and prey production in Lake Erie, we generated annual estimates of population-wide walleye prey consumption during 1986–1995, quantifying year-to-year variability in the importance of temperature regime and walleye population structure and population size to predatory demand.

Materials and methods

Study approach

By combining long-term empirical estimates of parameters and responses (estimated during 1986–1995) with simulation modeling, we quantify direct effects of observed (i.e., natural) variability in walleye population structure, level of consumption, and temperature regime on prey consumption and growth by Lake Erie walleye. Consideration of natural between-basin, among-year variability of these factors is very important in teasing apart their independent effects on walleye populations. For instance, both temperature regime and population structure differ between the western and central basins; through this modeling effort, we can test for their effects independently.

Specifically, we used a bioenergetics-based simulation model to track individual walleye during April through mid-November of a given year. Modeling individual walleye allowed us to represent

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Table 1. Design and description of parameter values for simulation experiments and lakewide consumption estimates.

	Model parameter			
	Population structure	Temperature regime	*p*	Population size
Simulation experiment I	**Year-specific** **Basin-specific**	Constant across years Constant across basins (1990 western basin)	Constant across years Constant across basins (mean across years from western basin)	Constant (20 000)
Simulation experiment II	Constant across years Constant across basins (1990 western basin)	**Year-specific** **Basin-specific**[a]	Constant across years Constant across basins (mean across years from western basin)	Constant (20 000)
Simulation experiment III	**Year-specific** **Basin-specific**	**Year-specific** **Basin-specific**[a]	**Year-specific** **Basin-specific**	Constant (20 000)
Lakewide consumption	**Year-specific** **Basin-specific**	**Year-specific** **Basin-specific**[a]	**Year-specific** **Basin-specific**	**Year-specific (estimated by CAGEAN)**

Note: Model parameters whose effects are being tested in a given experiment are shown in bold. Actual parameter values are derived from empirical measurements in Lake Erie, 1986–1995 (see Materials and methods).

[a]Includes migratory population in which walleye move between the western and central basins.

physiological processes of individual fish and permitted direct extrapolation to the entire population. Simulation experiments were designed to determine the effects of walleye population structure (age and size structure), annual temperature cycle, and age-specific consumption on walleye growth and consumption (Table 1). To examine growth of walleye from basin-specific and migratory populations, simulation experiments had three distinct walleye population treatments: (*i*) population remaining in the western basin for the entire growing season, (*ii*) population remaining in the central basin for the entire growing season, and (*iii*) a population migrating from the western to the central basin in early June and returning in early September. Characterizing walleye populations as either basin specific or migratory is very important, given differences in temperature regime between Lake Erie's western and central basins. With rapid spring warming rates, no depth stratification (i.e., well-mixed waters), and high summer water temperatures, the western basin of Lake Erie represents a very different growing environment than the central basin, which warms later in the year, stratifies normally, and generally has lower summer water temperatures. Thus, residence within a given basin or seasonal movement between the western and central basins will significantly influence walleye growth and consumption.

Characterizing daily temperature regimes

Annual basin-specific temperature regimes were generated to simulate the temperature regime that a western basin, central basin, or migratory walleye might experience during the growing season, which we defined as 1 April through 15 November. Daily basin-specific estimates of surface water temperature (depth <1 m) represent means taken from multiple point estimates of temperature from that basin. Temperature data were received from multiple state, federal, and provincial agencies (Sandusky and Fairport fisheries stations, ODNR-ODW; St. Lawrence Basin Project, National Water Research Institute, and Lake Erie Management Unit (Ontario Ministry of Natural Resources); Monroe Water Authority (Monroe, Mich.); National Oceanic and Atmospheric Administration CoastWatch (Great Lakes Environmental Research Laboratory)). When combined, these data sets provide widespread spatial coverage of surface water temperatures within a basin, allowing us to generate realistic basin-wide temperature estimates for any given day within a year during 1986–1995. If no temperatures were recorded for a given day, we assumed that the temperature from the previous day described that day. To simulate the thermal regime experienced by migratory walleye, we constructed a temperature data set that was a composite of western and central basin temperature regimes. To match the apparent timing of this seasonal movement, western basin temperatures were used for 1 April through 31 May, central basin temperatures were used for 1 June through 31 August, and western basin temperatures were used for 1 September through 15 November (M. Turner (ODNR-ODW), R. Haas (Michigan Department of Natural Resources), and S. Nepszy (Ontario Ministry of Natural Resources), unpublished tagging data).

Characterizing simulated walleye populations

Simulated walleye populations were composed of age-classes 2 through 10+. Reliable population estimates were not available for walleye younger than age 2; thus, they were excluded. Annual walleye age structure (proportion of the population within a given age-class) in Lake Erie was generated by catch-at-age analysis (i.e., CAGEAN; Deriso et al. 1985) conducted by the Walleye Task Group of the Lake Erie Committee, Great Lakes Fishery Commission, modified to include fish age 7 through 10+. We assumed that age structure was constant among western basin, central basin, and migratory walleye populations. Age- and sex-specific size structure data (length–frequency and weight–frequency distributions) were obtained from annual ODNR-ODW fall gillnet surveys. Walleye from a given age-class and sex were grouped according to 10-g weight increments, and we calculated the proportion of individuals in a given weight-class for each age-class and sex. To generate representative weight distributions for walleye in age-classes 7 through 10 (age-classes traditionally underrepresented in gillnet samples), we pooled all individuals of these ages captured in fall gillnet sampling across all years of interest (1986–1995). From these data, we were able to construct robust weight distributions representative of these older walleye.

Coupling age and size structure information, we generated simulated walleye populations (N = 20 000 individual walleye, characterized by a 50:50 sex ratio) in which walleye were randomly (using the RAN2 subroutine; Press et al. 1989) assigned to an age-class in proportion to the age composition of the population for a

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specific year. Next, each simulated walleye was assigned to a 10-g age- and sex-specific weight-class in proportion to the weight–frequency distribution for that age-class and sex. Once assigned to an age/sex/weight-class, the exact weight of each walleye within the 10-g weight-class was randomly chosen (using RAN2; Press et al. 1989) from a uniform distribution.

Based on weight-at-age, female walleye grow faster than male walleye, resulting in sexual dimorphism. To determine if female walleye grew more because of higher consumption rates, we examined sex-specific consumption patterns for Lake Erie walleye and found that females did exhibit greater weight-specific consumption. Alternatively, females may feed more frequently than males; however, our analyses could not assess this possibility.

Factors influencing sexual dimorphism have been investigated for a closely related percid, yellow perch, in which estrogenic compounds stimulate female growth, whereas androgenic compounds retard male growth rates (Malison et al. 1985, 1988). For both sexes, these changes in growth rate were related to maturation. For walleye, we assumed that similar hormonal effects may be driving the apparent sexual dimorphism. Given that the physiological mechanism for sex-specific differences was unknown, we did not change parameters associated with walleye consumption rate. Rather, we adjusted the daily growth increment of female walleye. Thus, we accounted for changes in weight-specific consumption indirectly by increasing growth rate rather than consumption (as we found no evidence for male–female differences in consumption rate).

To determine the appropriate adjustment, we used fall weight-at-age data (from walleye captured in ODNR-ODW fall gillnet surveys) to calculate the sex-specific change in mean weight for a given age-class of walleye on an annual time step. We used these data to estimate constant annual growth increments for males (eq. 1) and females (eq. 2):

$$(1) \qquad X_{t+1,\sigma^{\prime}} = X_{t,\sigma^{\prime}} + \Delta_{\sigma^{\prime}}$$

$$(2) \qquad X_{t+1,\varphi} = X_{t,\varphi} + \Delta_{\sigma^{\prime}} + \omega$$

where $X_{t,i}$ is mean wet weight of individuals of sex i in a given walleye age-class in October of year t, $\Delta_{\sigma^{\prime}}$ is the estimated annual growth increment for male walleye (i.e., change in wet weight from year t to year $t + 1$), and $\Delta_{\sigma^{\prime}} + \omega$ is the estimated annual growth increment for females. Based on inspection of data associated with multiple walleye age-classes, we assumed that ω was a constant value over all ages and initial sizes, with a value of $\omega = 100$ g·year^{-1}. Given that the simulation model uses a daily time step, eq. 1 was converted to growth on a daily time step:

$$(3) \qquad X_{t,u+1,\sigma^{\prime}} = X_{t,u,\sigma^{\prime}} + d_{\sigma^{\prime}}$$

where $X_{t,u,\sigma^{\prime}}$ is wet weight of a male walleye on simulation day u in year t and $d_{\sigma^{\prime}}$ is the constant daily growth increment for male walleye (i.e., change in wet weight from day u to day $u + 1$), calculated via the bioenergetics component of the simulation model. Thus, on each simulation day, weight-specific consumption (and thus, daily growth increment) was calculated in the same fashion for male and female walleye. To account for the higher level of growth associated with female walleye, we converted ω to a daily growth adjustment α of 0.4386 g·day^{-1} ($\alpha = \omega/228$ simulation days) and added α to the bioenergetics-calculated female walleye weight at the end of each simulation day:

$$(4) \qquad X_{t,u+1,\varphi} = X_{t,u,\varphi} + d_{\sigma^{\prime}} + \alpha$$

Calculating age-specific *p* values

Walleye prey consumption was modeled using the p value, a scaling factor used in bioenergetics modeling (Hewett and Johnson 1992). The p values are weight and temperature dependent and represent the proportion of maximum daily feeding rate attained by an individual fish. For example, a walleye that feeds at 100% of its maximum feeding rate will have a p value of 1.0, whereas one that feeds at 40% of its maximum feeding rate will have a p value of 0.4. We back-calculated annual, age-specific p values (using the bioenergetics model; Hewett and Johnson 1992) for walleye in each basin by combining observed growth of walleye captured in ODNR-ODW fall gillnet surveys with annual temperature regimes. For example, we used the bioenergetics model to estimate the p value required to grow a fish from the mean weight of age-2 walleye in October 1991 gill nets to the mean weight of age-3 walleye in October 1992 gill nets, given the 1992 western basin temperature regime. Age-specific p values were kept constant for a given simulation year.

Simulation experiment I: influence of walleye population structure

The first simulation experiment examined the influence of walleye population structure (age and size structure) on patterns of walleye growth and consumption. Walleye population structure may be important in determining consumptive demand due to substantial annual variability in walleye abundance and population biomass resulting from among-year variability in year-class strength. In this experiment, we compared growth (change in population biomass during the growing season) and consumption (total consumption by the walleye during the growing season) of modeled walleye populations having empirically measured age and size structures characteristic of either the western or central basin population. We simulated walleye population structure for each year during 1986–1995 keeping temperature regime and age-specific consumption levels constant among all years (Table 1). We used the 1990 western basin temperature regime and parameterized age-specific consumption using western basin p values, averaged across all calculated values for each age-class among years. Because we did not know the population structure of the migratory walleye population, the first simulation experiment was done only for western and central basin population treatments.

Simulation experiment II: influence of temperature regime

The second simulation experiment focused on the independent influence of annual temperature regimes on patterns of walleye growth and consumption. In this experiment, we compared growth (change in population biomass during the growing season) and consumption (total consumption by walleye during the growing season) of modeled walleye experiencing empirically estimated temperature regimes characteristic of the western basin, central basin, or migratory populations. We simulated temperature regimes for each year during 1986–1995 for all three population treatments, keeping initial population structure and age-specific consumption levels constant among all years (Table 1). We used the age and size structure of the 1990 western basin walleye population to create a single initial population that was used in each run of this simulation experiment. Finally, we parameterized age-specific consumption using western basin p values, averaged across calculated values for each age-class among all years.

Simulation experiment III: combined effects of population structure, age-specific consumption, and temperature regime

The third simulation experiment focused on the combined effects of walleye population structure, age-specific consumption level, and annual temperature regime on year-specific patterns of walleye growth (change in population biomass during the growing season) and consumption (total consumption by walleye during the growing season). We used initial walleye population structure, consumption level, and annual temperature regime measured empiri-

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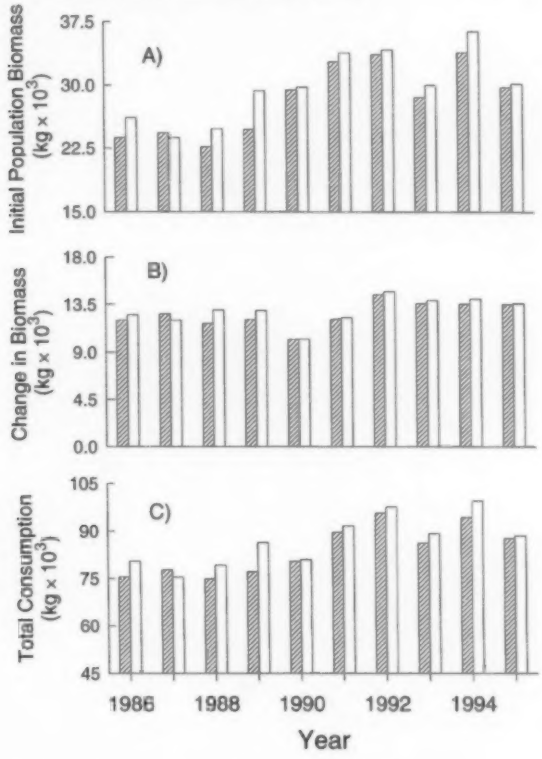
Fig. 1. Simulation results for the effects of walleye population structure on walleye growth and consumption during 1986–1995 in the western and central basins of Lake Erie (simulation experiment I). Individual population treatments are the western basin (hatched bars) and central basin (open bars) populations. (A) Initial population biomass for simulated walleye populations across years. (B) Change in population biomass for simulated walleye populations across years. (C) Total consumption by simulated walleye populations across years.



cally for each year and population treatment (Table 1). Because we did not have estimates of population structure for the migratory walleye population, we used the age and size structure of the western basin population to characterize the initial size distribution of migratory walleye populations.

Estimating lakewide prey consumption by walleye

By coupling age-specific estimates of daily consumption generated by simulation experiment III with annual CAGEAN population estimates (Table 1), we estimated lakewide prey consumption by walleye populations during 1986–1995. For these estimates, we assumed that the age and size structure of simulated populations was representative of the lakewide walleye population. As noted previously, age-0 and age-1 walleye were not included in these analyses due to inadequate empirical data; if we included these age-classes, predatory demand estimates likely would increase somewhat. When describing "lakewide" walleye populations, we are referring specifically to western and central basin walleye stocks. CAGEAN population estimates are calculated based solely on western and central basin data, simply due to the fact that the eastern basin walleye stock appears to be quite small. Given the lack of information regarding the proportion of the lakewide population that can be characterized as western basin, central basin, or migratory walleye, we conducted separate lakewide consumption estimates for each population treatment. We also conducted a fourth extrapolation assuming that the lakewide walleye population was divided equally among the three population treatments. We generated annual estimates of lakewide consumption (LWC) for each extrapolation:

$$(5) \qquad \mathrm{LWC} = \sum_{i=91}^{319} \sum_{j=2}^{10} \left(\frac{C_{ij}}{n_j} \times N_j \right)$$

where i is day of the year (range = 91 (1 April) through 319 (15 November)) and j is age-class (range = 2 through 10). Daily consumption per lakewide walleye in age-class j was calculated by dividing daily consumption by all simulated walleye in age-class j (C_{ij}) by the abundance of simulated walleye in age-class j (n_j) and then multiplying this value by the CAGEAN estimate of the lakewide abundance of age-class j (N_j). Year-specific estimates of consumption by the lakewide walleye population were generated by summing consumption by all age-classes across all days in a given year.

Results

Simulation experiment I: influence of walleye population structure

This experiment focused on the effects of walleye population structure (age and size structure) on among-year variability of basin-specific growth and consumption. Basin-specific initial population biomass was quite variable among years (Fig. 1A). In general, central basin populations had higher initial population biomass (Fig. 1A) and slightly larger increases in biomass (Fig. 1B) and total consumption during the growing season (Fig. 1C) than western basin populations because central basin walleye were generally larger than western basin walleye at the beginning of the growing season.

To account for basin-specific differences in initial biomass and to determine if there was a consistent basin-specific advantage relative to growth rate, we calculated a basin-specific mean for the change in population biomass (final biomass minus initial biomass) for each population treatment across all simulation years. The mean (among-year) change in biomass growth did not differ between the western and central basin populations as a function of walleye population structure alone (Table 2).

Simulation experiment II: influence of temperature regime

The second simulation experiment focused on the influence of temperature alone on patterns of walleye growth and consumption. In this case, walleye population structure was held constant among all population treatments and across all simulation years. Within a population treatment, final population biomass varied greatly among years, primarily due to variation among years in growth during summer (Fig. 2). Spring and fall growth differed little among years. This among-year variation in walleye biomass accrual during summer was much higher in the western basin than in the central basin or migratory population treatments, leading to higher among-year variability in western basin walleye growth rates (Fig. 2).

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Table 2. Mean (±1 SE) change in population biomass (final biomass (kg) minus initial biomass (kg); mean taken across all simulation years) in each simulation experiment for western basin, central basin, and migratory (between western and central basins) walleye populations in Lake Erie.

	Western basin walleye populations	Central basin walleye populations	Migratory walleye populations
Simulation experiment I	12 558 (±386)	12 898 (±400)	Not simulated
Simulation experiment II	9 890 (±1070)	12 610 (±582)	13 470 (±436)
Simulation experiment III	12 035 (±1384)	12 981 (±1219)	16 151 (±1970)

Fig. 2. Population biomass trajectories (1 April through 15 November) resulting from the effects of temperature regime only (across all simulation years; simulation experiment I) for (A) western basin, (B) central basin, and (C) migratory (western and central basins) population treatments in Lake Erie. In cases where individual lines were too close together to distinguish, the lines are grouped and listed in order of decreasing final population biomass.

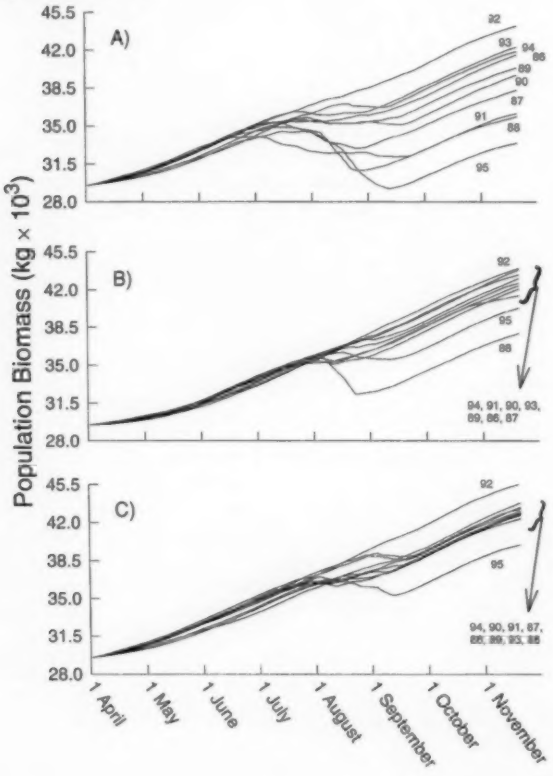
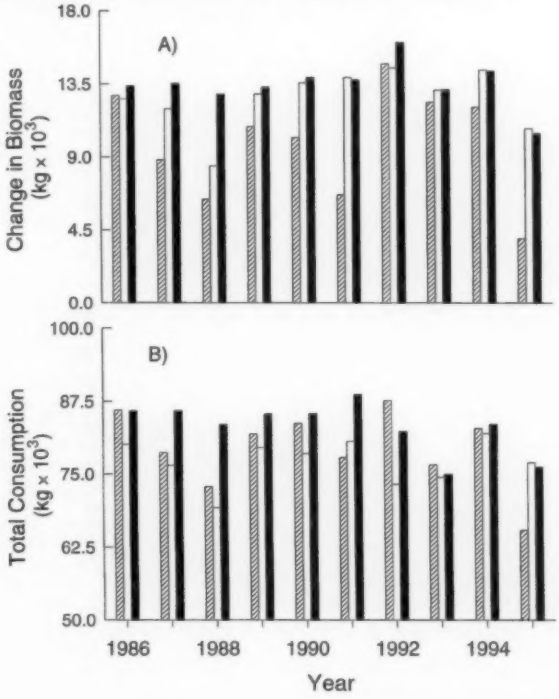


Fig. 3. Simulation results for the effects of temperature regime on walleye growth and consumption during 1986–1995 in the western and central basins of Lake Erie (simulation experiment II). Individual population treatments are the western basin (hatched bars), central basin (open bars), and migratory populations (solid bars). (A) Change in population biomass for simulated walleye populations across years. (B) Total consumption by simulated walleye populations across years.



Migratory walleye populations grew most quickly (measured as the change in population biomass during the growing season) in nearly all simulation years, with central basin populations growing only slightly less (Fig. 3A). In contrast, western basin walleye populations had the lowest and most variable levels of growth of all the population treatments across simulation years (Fig. 3A).

In most simulation years, migratory walleye populations consumed the most (summed across the growing season), followed by western basin populations (Fig. 3B). Interestingly, whereas western basin walleye generally consumed more than central basin walleye (Fig. 3B), they also grew less in terms of biomass accrual (Fig. 3A). Lower growth in the western basin may derive from temperatures that generally exceeded optimal temperatures for walleye growth during summer, leading to higher consumption, but reduced growth.

To determine if a treatment-specific growth advantage existed due to temperature regime alone, we calculated a basin-specific mean for the change in biomass (measured as the change in population biomass during the growing season) for each population treatment across all simulation years. In general, both migratory and central basin walleye grew more quickly than western basin walleye (Fig. 3B). High growth in migratory populations may derive from these walleye ex-

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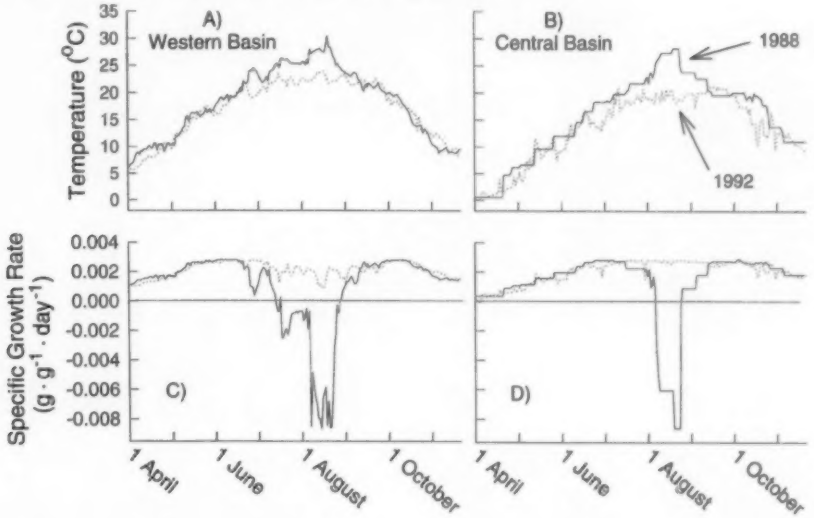
Fig. 4. Temperature regimes of the (A) western and (B) central basins of Lake Erie in 1988 (solid line) and 1992 (broken line) and specific growth rate for a 1000-g walleye feeding at a constant p value (0.4) as a function of the 1988 (solid line) and 1992 (broken line) temperature regimes in the (C) western and (D) central basins of Lake Erie.



ploiting growth opportunities in both basins, given that the western and central basins warm at different rates.

To further illustrate how year-specific temperature regimes influence walleye growth, we examined temporal trends of modeled walleye growth rate (grams per gram per day, calculated using the bioenergetics model for a 1000-g walleye feeding at a p value of 0.4) during the 1988 and 1992 growing seasons, years having very different temperature regimes (Fig. 4). In 1988 and 1992, early-season growth was highest in the western basin, owing to faster warming rates than in the central basin. However, by early June, central basin growth surpassed western basin growth, primarily because western basin temperatures exceeded optimal temperatures for walleye growth (Fig. 4). Strong year-to-year variability in temperature regime influenced walleye growth rates. For example, during 1988, modeled growth in both basins became negative during late summer as water temperatures approached 31°C (Fig. 4). In contrast, during 1992, a cool year in which water temperatures rarely exceeded 24°C, walleye growth rates (simulated) were positive through the entire growing season in both basins (Fig. 4).

Simulation experiment III: combined effects of population structure, age-specific consumption, and temperature regime

The third simulation experiment focused on the combined effects of walleye population structure, age-specific consumption level (as estimated by p values), and annual temperature regime on patterns of walleye growth and consumption. Differences among years in final population biomass could be attributed to differences in initial population biomass and differences in growth rates during all seasons (Fig. 5). In contrast with simulation experiment II (effects of temperature regime), among-year differences in final population biomass were not driven solely by differences in summer growth trajectories (Fig. 5).

Initial population biomass for the simulated walleye populations was variable among years and highest in the 1990's (Fig. 6A), primarily due to recruitment of large year-classes from the 1980s into older age-classes. In contrast with simulation experiments I and II, change in population biomass was highly variable (among years) across all three population treatments, with migratory walleye consistently growing more quickly than either the western or central basin populations (Fig. 6B). Interestingly, 1994 had the highest initial population biomass but the lowest levels of consumption and growth across all simulation years (Fig. 6), a pattern not predicted by simulation experiments I and II. Total consumption also varied substantially among population treatments and simulation years; western basin and migratory populations generally had the highest consumption (Fig. 6C).

We calculated a mean change in biomass (measured as the change in population biomass during the growing season) for each population treatment across all simulation years. When year-specific walleye population structure, variable consumption, and temperature regime were incorporated into the model, migratory walleye populations maintained the high levels of growth conferred by temperature regime alone (Table 2). However, including these factors damped differences in biomass accrual between western and central basin walleye populations (Table 2). Interestingly, among-year variability in all population treatments increased substantially relative to the first two simulation experiments.

Estimating lakewide prey consumption by walleye

By coupling estimates of consumption from simulation experiment III with CAGEAN population estimates for each simulation year, we estimated lakewide consumptive demand for walleye populations during 1986–1995. Patterns of modeled lakewide consumption consistently tracked trends in walleye abundance (Fig. 7), with a peak in the late 1980's and a decline over the past 7 years. In general, population

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Fig. 5. Population biomass trajectories (1 April through 15 November) resulting from the combined effects of walleye population structure, age-specific consumption rates, and temperature regime (across all simulation years) for (A) western basin, (B) central basin, and (C) migratory (western and central basins) population treatments in Lake Erie (simulation experiment III). In cases where individual lines were too close together to distinguish either initial or final population biomass, the lines are grouped and listed in order of decreasing population biomass.

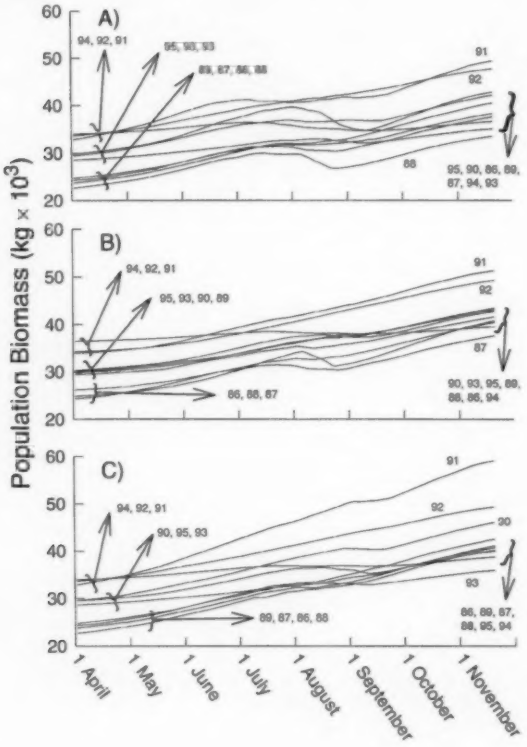
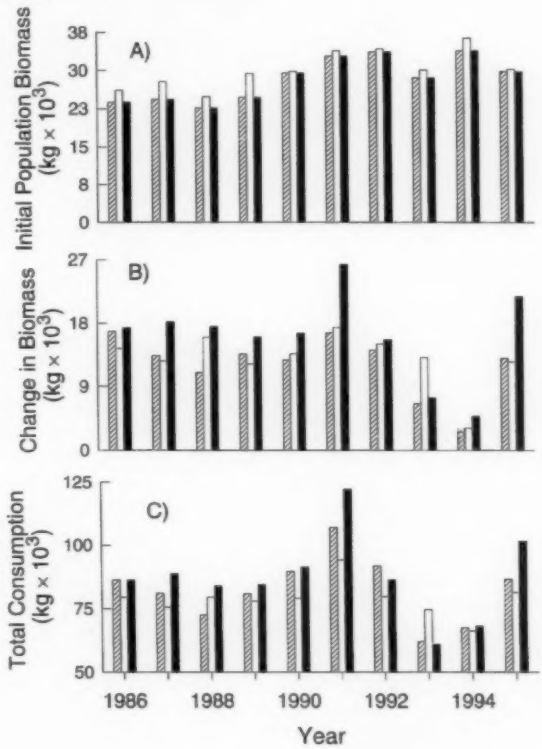


Fig. 6. Simulation results for the combined effects of walleye population structure, age-specific consumption rates, and temperature regime on walleye growth and consumption during 1986–1995 in the western and central basins of Lake Erie (simulation experiment III). Individual population treatments are the western basin (hatched bars), central basin (open bars), and migratory populations (solid bars). (A) Initial population biomass for simulated walleye populations across years. (B) Change in population biomass for simulated walleye populations across years. (C) Total consumption by simulated walleye populations across years.



treatment had little effect on estimates of lakewide consumption. The highest level of lakewide consumption by walleye occurred in 1988, which also had the highest population density of all simulation years (Fig. 7) and also had relatively low levels of growth and consumption (Fig. 6).

Discussion

Simulation experiment I: influence of walleye population structure

Interbasin differences in walleye age and size structure had limited influence on between-basin comparisons of annual consumption and growth. Empirical estimates of initial walleye population biomass were variable among years and consistently higher in the central basin than in the western basin. This, coupled with larger individual walleye in the central basin, generally resulted in higher estimates of modeled growth and total consumption for central basin populations relative to western basin populations. As initial population biomass varied among years, so did model estimates of total consumption. However, modeled growth rate (i.e., change in population biomass) did not exhibit high annual variability, nor did it differ greatly between basins. As large year-classes associated with the early to mid-1980's recruited to the lakewide population (resulting in increased initial population biomass), total modeled consumption also increased, demonstrating the importance of incorporating year-specific population structure when estimating the future consumptive demand of Lake Erie walleye.

Simulation experiment II: influence of temperature regime

Annual temperature regime strongly influenced patterns of consumption and growth by Lake Erie walleye. Western basin populations exhibited strong among-year variability in modeled consumption and growth, which was strongly related to among-year differences in summer temperature regime and its direct effects on walleye growth rate. Central basin walleye exhibited similar patterns of variability in

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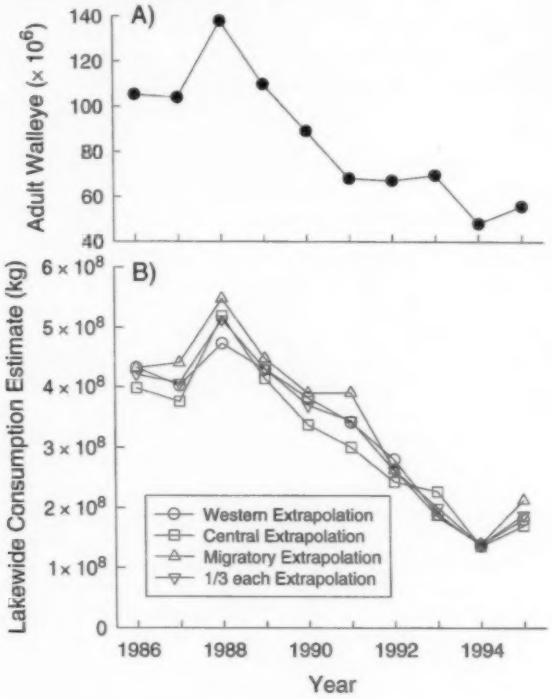
Fig. 7. Lake Erie (A) adult walleye (ages 2 through 10+) population size (estimated by CAGEAN) and (B) lakewide estimates of consumption by walleye extrapolated from simulation results during 1986–1995.



modeled consumption and growth, but to a lesser extent. In contrast, annual estimates of modeled consumption and growth rate for migratory walleye populations were remarkably stable. This stability derived from how the timing of interbasin walleye movement interacted with interbasin shifts of optimal growth temperatures (<24°C) for walleye. The western basin warms earlier than the central basin, and thus supports higher walleye growth rates early in the growing season. However, as water temperatures rise in early summer, growth peaks shift from the western to central basin, driving higher walleye growth in the central basin. Walleye that do not move between basins only experience a single growth peak, whereas migratory walleye exploit growth peaks in both basins. Interestingly, migratory timing, as quantified by tagging studies, occurs during early June (M. Turner (ODNR-ODW), R. Haas (Michigan Department of Natural Resources), and S. Nepszy (Ontario Ministry of Natural Resources), unpublished data), coincident with the basin-to-basin shift in growth peaks. Thus, with the timing of interbasin movement corroborated by tagging data, our modeling effort provides a strong explanation for seasonal walleye movements; simply put, migratory walleye will have higher growth rates. In fact, migratory walleye grew faster than central basin walleye (averaged among years), which grew faster than western basin walleye. In general, these simulation results indicate that year-specific, population-specific temperature regimes must be used when quantifying annual trends in walleye growth and consumption.

Summer temperature regime had a strong effect on modeled walleye growth rates in the western basin. In fact, summer water temperatures can be quite high for extended periods and may inhibit walleye growth. When water temperatures exceed 24°C, walleye growth rates decline (Momot et al. 1977). This decline is exacerbated by lack of access to a thermocline or hypolimnion (given that the western basin does not stratify). In contrast, summer water temperatures experienced by central basin and migratory walleye are generally lower, and although water temperatures can exceed 24°C, the duration and likelihood of these events are much lower than in the western basin. Thus, summer temperature regime is much less likely to limit central basin and migratory walleye growth than growth of western basin walleye.

Simulation experiment III: combined effects of population structure, age-specific consumption, and temperature regime

When we combined empirical, year-specific, population-specific estimates of walleye population structure, age-specific consumption rate, and temperature regime, we found different effects on modeled consumption and growth than when we examined effects of population structure and temperature in single-factor experiments (simulation experiments I and II). As in single-factor simulation experiments, all population treatments exhibited strong among-year variability in modeled consumption and growth, with migratory walleye having the highest values. Western and central basin walleye had similar levels of modeled growth; however, western basin walleye typically consumed more prey than central basin walleye. Walleye consumption and growth estimated in simulation experiment III were much lower in 1993 and 1994 than in other years. In contrast, simulation experiments I and II, examining effects of walleye population structure and temperature regime independently, did not predict reductions in consumption and growth for 1993 and 1994; thus, reduced levels of prey consumption likely slowed walleye growth rates during 1993 and 1994. Interestingly, the negative effects of summer temperature regime on western basin walleye growth were greatly reduced by the addition of year- and basin-specific population structure and age-specific consumption rates, indicating that the strong influence of summer temperatures can be damped or compensated for by these factors. Poor agreement between results of single-factor and multiple-factor simulation experiments illustrates the importance of combining information about population structure (an indicator of initial population conditions), consumption rates (a measure of prey availability), and temperature (an indicator of abiotic conditions) in estimating total consumption and growth.

The combined effects of population structure, age-specific consumption, and temperature regime resulted in substantially increased modeled growth rates (averaged among years) for migratory walleye relative to simulation experiments I and II. In contrast, modeled growth rates of nonmigratory walleye from central and, to a lesser extent, western basin populations were not much higher than observed in simulation experiments I and II but were much lower than observed in the migratory population treatment. Among-year variability associated with annual change in walleye population biomass (for all population treatments) increased rela-

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tive to single-factor experiments (simulation experiments I and II). Overall, these results suggest that we must combine empirical estimates of walleye population structure, temperature regime, and daily consumption with modeling to predict among-year differences in walleye consumption and growth.

As described in the Materials and methods section (under Characterizing simulated walleye populations), female walleye have higher growth rates than male walleye, possibly due to hormonal differences (Malison et al. 1985, 1988). We accounted for this in our simulation modeling through a female-specific daily growth adjustment and believe that this better estimates predatory demand associated with female walleye, which allows greater confidence in our estimates of population-wide predatory demand.

By combining long-term (10 years) empirical estimates of parameters and variables with simulation modeling, we parameterized simulations using actual estimates of natural variability in biotic and abiotic factors. Typically, modelers are limited to parameterizing a process using a calculated distribution (e.g., normal distribution) for variability estimates, whereas we actually tracked the effects of natural variability on model output (walleye consumption and growth) for a given basin–year combination. Empirical estimates of water temperature, walleye age and size structure, and walleye population size were derived from regular, long-term, standardized monitoring programs conducted by state and federal agencies on Lake Erie. Without these monitoring data as model inputs and parameters, we would have been unable to account for natural variability of biotic and abiotic factors in our simulations.

Predatory demand by Lake Erie walleye

To provide insight into among-year variability of walleye predatory demand, we used annual estimates of walleye population size to extrapolate from our simulated consumption data to consumption by the entire population. Estimated total consumption by western and central basin Lake Erie walleye populations was highest in 1988. However, simulation experiment III suggests that the walleye population of 1991 had a much larger consumptive demand per walleye than did the walleye population of 1988. This difference between simulation results (based on 20 000 walleye) and lakewide consumption estimates (1988, based on 138 million walleye; 1991, based on 68 million walleye) illustrates the importance of accounting for the interaction of lakewide walleye population size with population structure, age-specific consumption rates, and temperature regime when estimating predatory demand. In other words, while population structure, consumption rates, and temperature regime certainly set the potential for years of high consumptive demand, we must consider the cumulative predatory impact of the lakewide population. Thus, even when predatory demand per individual walleye is low, the existence of a large walleye population can drive predatory demand to exceed the capacity of prey supply to support high levels of walleye growth and reproductive potential.

When considering the relationship between predatory demand and prey production in systems with stocked or introduced top predators, the traditional focus has been on the possibility that predatory demand will exceed prey availability, leading to the collapse of prey populations and, ultimately, predator populations (Stewart et al. 1981; Stewart and Ibarra 1991; Jones et al. 1993; Kitchell et al. 1997). However, in systems where predator populations are naturally reproducing, rather than stocked, production of new predator year-classes is likely a function of energy available from prey populations. Thus, there is a natural feedback mechanism in place to buffer predator population growth in the face of low prey availability, allowing prey stocks to recover.

In Lake Erie, strong feedbacks exist between naturally reproducing walleye and their prey; recent evidence suggests that walleye populations rapidly reduce their reproductive output in response to reduced prey availability. Underlying this response is the strong association between fall growth and energetic condition of Lake Erie's walleye spawning stock and subsequent age-0 year-class strength (Henderson and Nepszy 1994). The importance of fall growth to reproductive potential is not surprising, as gonadal development (i.e., vitellogenesis, spermatogenesis) is nearly complete by late fall – early winter (Malison et al. 1994; Malison and Held 1996). Whether female walleye spawn in spring is apparently determined by the level of surplus energy for allocation to vitellogenesis during the previous autumn (Henderson and Nepszy 1994). Surplus energy, and consequently, age-0 year-class strength, appears to be strongly related to the fall availability of lipid-rich gizzard shad, preferred walleye prey (Madenjian et al. 1996). In fact, during 1979–1993, fall gizzard shad abundance alone explained 42% of the variation in walleye age-0 year-class strength the following spring, contributing substantially to a model (also including parental stock size and spring warming rate) that explained 92% of the variability in walleye recruitment (Madenjian et al. 1996).

Given that prey fish production in Lake Erie exhibits high among-year variability (Knight and Vondracek 1993), this feedback mechanism has significant implications. Reductions in the availability and quality (e.g., energy density, lipid content) of the prey base likely reduce age-0 walleye production and success in the subsequent year, reducing the potential for substantial short-term (age 0) and long-term (lifetime) additions to population-wide predatory demand. Thus, the rapid (no time lag) reproductive response by walleye to reduced prey availability can defuse potentially explosive predator population growth (where overgrazing of the prey resource is possible) by allowing recovery of prey populations via a reduction in predation pressure on juveniles and adults of many prey species.

Although this feedback mechanism allows rapid reproductive response to low prey availability, it has limited influence on the predatory demand of the extant adult walleye population. Thus, to understand predatory demand, we must consider the predatory inertia of a population (Stewart et al. 1981; Carpenter et al. 1985). Given that walleye are long lived, the predatory demand associated with large cohorts will be exerted on Lake Erie for the entire life span of that year-class (exceeding 12 years, up to 18 years), regardless of prey availability. Therefore, the temporal scale associated with the predatory capabilities of a large walleye year-class differs from the shorter life spans and reproductive response of the prey assemblage. Thus, when prey availability is low,

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the extant walleye population may still exceed the capacity of prey production to support it despite the rapidity of the feedback associated with reduced walleye reproductive potential.

While this study is the most current estimate of predatory demand in Lake Erie, our work only represents the consumptive demand of a single species, walleye. If we estimated cumulative predatory demand by all Lake Erie piscivores (e.g., walleye, smallmouth bass (*Micropterus dolomieu*), burbot (*Lota lota*), lake trout (*Salvelinus namaycush*), white bass), the probability of predatory demand exceeding prey availability (or its capacity to support high growth and successful reproduction by these species) would likely increase, particularly when prey abundance is low. While rarely measured, community-level predatory demand (i.e., summed across all piscivores) may prove to be a significant structuring force in aquatic ecosystems. For example, in northern Wisconsin lakes, the combination of offshore walleye populations and inshore northern pike (*Esox lucius*) populations drove prey to low densities (Kempinger and Carline 1977), lower than with a single predator. Essentially, prey had no habitat refuge from predation; both inshore and offshore represented significant mortality risks. In this case, predator biomass was not as important as the type of predators added (Kempinger and Carline 1977). In other words, as the number of predator species increases, the availability of spatial and temporal refuges for prey declines, increasing the probability of prey fish mortality. Overall, increased predator biomass combined with reductions in the availability of prey refuge may lead to predators exceeding system carrying capacity.

Concluding comments

With recent shifts in the dynamics of lake productivity (Knight 1997), both biotic and abiotic characteristics of Lake Erie have changed substantially (Makarewicz and Bertram 1991). Coupling changes in the Lake Erie ecosystem with recent advances in our understanding of predator–prey interactions, management of walleye and their associated prey has become a significant challenge. For example, while the natural feedback mechanism between predatory demand and prey availability has a rapid effect on walleye reproductive potential, it has limited immediate effects on extant walleye predatory inertia. The complicated nature of these interactions truly creates a dilemma for our understanding and management of the relationship between predatory demand and prey availability. Similarly, given the implications of community-level predatory demand for prey availability, an understanding of the predatory capabilities of other Lake Erie predators, particularly increasing smallmouth bass and burbot populations, seems critical. Given the dependence of Lake Erie predators (particularly walleye) on the prey assemblage, we should focus future research on the influence of biotic and abiotic variability on prey fish recruitment and attempt to identify time lags associated with predator–prey responses to prey fish production. Continued monitoring of the fish community with standardized assessment programs is critical for future insight into predatory demand in Lake Erie. Only by incorporating these data into the decision-making process can we truly assess the balance between predatory demand and prey availability (Ney 1990). In recognition of Lake Erie's changing trophic conditions, the Lake Erie Committee of the Great Lakes Fishery Commission drafted fish community objectives that support management of food web structure and maintenance of a diverse forage base to sustain production by predators, particularly walleye (Lake Erie Committee 1997). To achieve long-term stability and sustainability of Lake Erie's walleye population and prey fish assemblage, fishery managers may need to regulate predatory demand among all piscivores, as opposed to walleye alone.

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Impacts and efficiency of scallop dredging on different soft substrates

David R. Currie and Gregory D. Parry

Abstract: Impacts of scallop dredges and their efficiency were examined experimentally in three areas with different soft substrates in Port Phillip Bay, southeastern Australia. Physical and biological changes were measured on large (600 × 600 m) experimental plots that were dredged with an intensity and duration similar to normal fishing operations. Dredges were most efficient on soft, flat, muddy sediments (51–56% of commercial-sized scallops caught) and least efficient on firm, sandy sediments with more topographic variation (38–44%). Dredging flattened all plots, but changes to topography were most apparent on plots dominated initially by callianassid mounds. Dredges caught predominantly the scallop *Pecten fumatus*, and damage to bycatch species was slight, except for high mortality rates (>50%) of spider crabs and the probable mortality of many discarded ascidians. Changes to benthic community structure caused by scallop dredging were small compared with differences between study areas, and even marked reductions in the size and longevity of scallops over the last two decades may not be due entirely to dredging. The recent cancellation of all scallop dredging licences offers a unique opportunity to determine the contribution of scallop dredging to ecological changes in the bay over the past 30 years.

Résumé : Les impacts des dragues à pétoncles et leur efficacité ont été étudiés expérimentalement dans trois secteurs présentant des substrats mous différents dans la baie de Port Phillip, dans le sud-est de l'Australie. On a mesuré les changements physiques et biologiques dans de grandes parcelles expérimentales (600 × 600 m) qui ont été draguées avec une intensité et pour une durée semblables à celles des opérations normales de pêche. Les dragues étaient plus efficaces sur les sédiments mous, plats et vaseux (51 à 56% des pétoncles de taille commerciale capturés) et moins efficaces sur les sédiments fermes sableux présentant plus de variations topographiques (38–44%). Le dragage a aplati toutes les parcelles, mais les changements topographiques étaient plus apparents dans les parcelles dominées initialement par les monticules des callianassidés. Les dragues ont surtout capturé le pétoncle *Pecten fumatus*, et les dommages aux espèces des prises accessoires étaient peu importants, sauf dans le cas des araignées de mer (taux de mortalité élevés, >50%) et de nombreuses ascidies rejetées qui sont probablement mortes. Les changements dans la structure des communautés benthiques causés par le dragage des pétoncles étaient peu importants en comparaison des différences entre les secteurs de l'étude, et même les réductions marquées de la taille et de la longévité des pétoncles au cours des deux dernières décennies ne peuvent être entièrement attribuées au dragage. L'annulation récente de tous les permis de dragage des pétoncles offre une occasion unique pour déterminer la contribution de cette pêche aux changements écologiques survenus dans la baie au cours des 30 dernières années.

[Traduit par la Rédaction]

Introduction

Despite the long history of concern about the effects of dragging fishing gear along the seafloor (De Groot 1984), few impacts of dredging and trawling have been well documented. Previous studies of these fishing impacts indicate that physical effects depend on the softness of sediments and the weight of gear (Caddy 1973), while biological effects depend on the vulnerability of the communities present and, particularly, on the amount of epibiota in the area being fished (Bradstock and Gordon 1983; De Groot 1984; Peterson et al. 1987; Van Dolah et al. 1987; Sainsbury 1988; Collie et al. 1997). Increased environmental awareness has focused attention on a range of potential impacts of shellfish dredging (reviewed by Messieh et al. 1991; Jones 1992; Currie and Parry 1996) but particularly on the need to more adequately assess biological impacts. These impacts are difficult to investigate because of the complexity of biological communities and our limited knowledge of their natural variability (Messieh et al. 1991). Biological impact studies are also usually costly (Gislason 1994), and because they require closure of commercial fishing grounds to create unfished areas, they are frequently opposed by the fishing industry. These difficulties have caused compromises in the design of most studies. Comparisons of areas with historically different intensities of fishing have been made (Graham 1955; BEON 1992; Collie et al. 1997), but in these studies the effects of fishing cannot be distinguished from spatial differences unrelated to fishing. In other studies, experimental fishing has involved disturbances of such small areas (McShane 1981; Eleftheriou and Robertson 1992; Thrush et al. 1995) that the relevance of these studies to large-scale commercial operations is uncertain.

The Port Phillip Bay, southeastern Australia, scallop fish-

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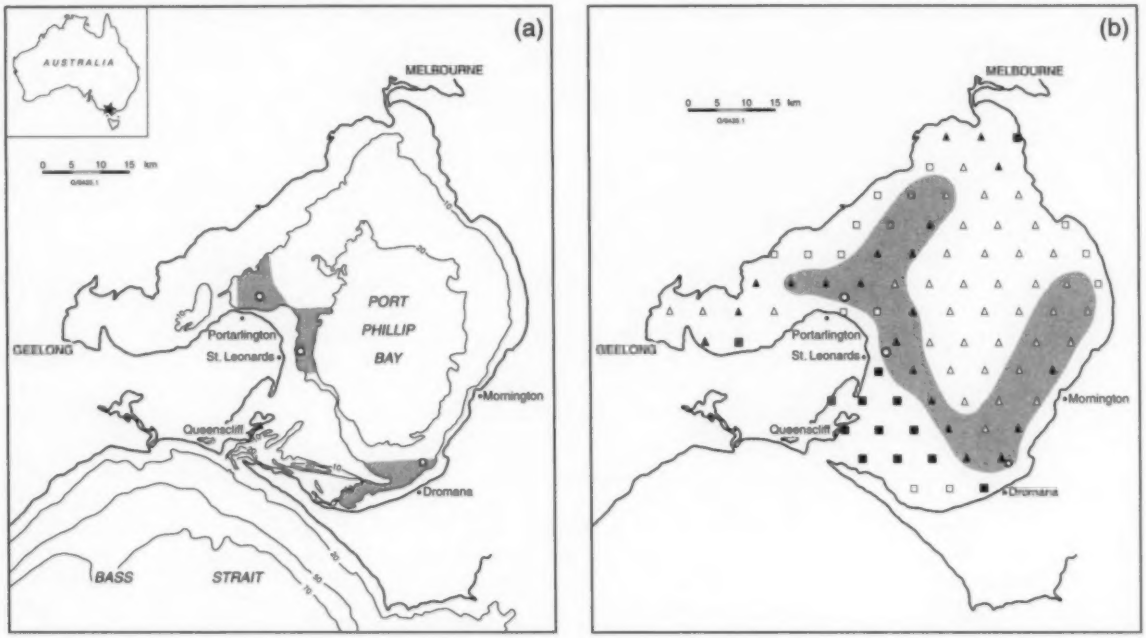
Fig. 1. (*a*) Location of the study area showing dredge plots (○) and areas closed to scallop dredging during 1991 (shaded). (*b*) Infaunal communities in Port Phillip Bay (from Currie and Parry 1999). ■, Low-diversity sands; □, high-diversity sands; ▲, intermediate sediments; △, central muds. Stippled symbols are seagrass communities. The location of dredge plots (○) at each study area and the main scallop grounds (shaded) are shown.



ery commenced in 1963 and catches and dredging intensity increased dramatically until the fishery collapsed in 1968 (Gwyther and McShane 1988). The intensity of dredging in the 1990's was lower than in the early years of the fishery, but 84 vessels were still licensed to dredge for scallops in Port Phillip Bay in 1996. All but the shallowest regions of the bay have been dredged, but with varying intensities. Scallop dredging occurred mostly in depths between 10 and 20 m (Fig. 1*a*) and was illegal in areas shallower than 10 m in the east and 5 m in the west of the bay after 1985. In 1997, after this study was completed, all scallop licences were cancelled because of public concern about the environmental effects of scallop dredging.

This study was designed to assess short-term impacts of dredging in different areas, rather than the cumulative ecological effects of 30 years of scallop dredging. Three large areas of Port Phillip Bay were closed to all scallop dredging throughout 1991 (Fig. 1*a*). In each closed area, a large experimental plot was dredged by commercial fishers with an intensity that was typical of either heavy or very heavy dredging, based on historical levels of dredging in the bay. Dredging-related changes to epifauna in all three areas and infauna in one area were examined using a BACI (before, after, control, impact) experimental design (Stewart-Oaten et al. 1986). The expense of this large-scale experiment meant that in the other two areas, dredging-related changes to infauna were assessed using only uncontrolled BAI comparisons. Related studies assessed the duration of impacts on infauna (Currie and Parry 1996), effects on fish communities (G.D. Parry and D.R. Currie, in preparation), and the extent of sediment disturbance by dredging (Black and Parry 1994, 1999).

In addition to investigating environmental impacts, the efficiency of dredges used to collect scallops in Port Phillip Bay and the damage they caused to the catch were also measured in each study area. These studies were considered important because inefficient dredges may cause more damage, as they must be dragged over larger areas. Previous studies had suggested that the dredges used in Port Phillip Bay were very inefficient (12%) and could cause massive damage to nonharvested scallops (McLoughlin et al. 1991).

Methods

Study design

Throughout 1991, three large areas (30–40 km^2) in Port Phillip Bay near Dromana, Portarlington, and St. Leonards were closed to all scallop dredging (Fig. 1*a*). Closed areas were policed effectively by fisheries enforcement officers, visited frequently in the course of this research, and strongly supported by the scallop industry. We are confident that no illegal scallop dredging occurred in any closed area. Areas were chosen to represent a wide range of sediment types in the 10–20 m depth zone where most commercial scallop fishing occurred (Fig. 1*b*). The sediments varied from medium sand (sensu Friedman and Sanders 1978, phi = 2) at Dromana to fine sand (phi = 3–4) at St. Leonards and coarse silt (phi = 5–6, excluding the considerable amount of coarse shell material present) at Portarlington (Rosenbaum et al. 1992; Black and Parry 1994; Greilach et al. 1995).

Two 600 × 600 m experimental plots were located in each closed area. At St. Leonards, plots were adjacent in a depth of 12–

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Table 1. Mean catch rates of scallops and bycatch species (mean no./drag) and number of drags during each days dredging on experimental plots at Dromana, Portarlington, and St. Leonards (all dredging was undertaken during 1991).

	Dromana		Portarlington				St. Leonards		
Species	26 Aug.	28 Aug.	20 Nov.	21 Nov.	10 Dec.	11 Dec.	16 July	17 July	18 July
Pecten fumatus ≥70 mm	264	186	760	466	286	207	93	72	59
P. fumatus <70 mm	397	328	1206	908	627	653	92	82	30
P. fumatus damaged	5.0	5.1	2.5	5.3	1.0	1.9	0.4	0.7	0.3
Ostrea angasi clumps	208	204	1.0	0.8	0.9	0.7	10.3	9.8	11.8
Pyura stolonifera	2.1	2.5	13.2	13.0	11.2	15.4	1.3	1.3	1.7
Herdmania momus	2.3	2.2	—	—	—	—	0.4	0.5	0.6
Cnemidocarpa etheridgii	0.4	0.6	3.0	3.3	2.3	3.7	0.4	0.7	0.3
Leptomithrax gaimardii	2.9	4.4	4.8	1.4	1.9	1.0	0.5	0.4	0.3
Stichopus mollis	0.01	—	3.3	2.4	1.1	1.3	0.06	0.08	0.01
Tosia magnifica	0.05	0.02	0.5	0.4	0.3	0.4	0.02	0.03	0.02
Costinasterias calamari	—	—	0.01	0.02	0.01	0.01	—	0.01	—
Octopus australis and *O. pallidus*	0.08	0.06	0.2	0.4	0.2	0.1	0.01	0.02	0.01
Austrosipho grandis	0.06	0.05	—	—	—	—	—	—	—
Hermit crabs (mostly *Trizopagurus strigimanus*)	0.08	0.06	—	—	—	—	0.02	0.03	0.04
Total nonbivalve epibiota (TNBE)	7.98	9.89	25.0	20.9	17.0	21.9	2.71	3.07	2.98
TNBE/*P. fumatus* ≥70 mm (%)	3.0	5.3	3.3	4.5	5.9	10.6	2.9	4.3	5.0
No. of drags	209	173	160	195	178	183	147	191	121

15 m, while at Dromana and Portarlington, they were 600 m apart in 14–16 and 13–15 m of water, respectively. In each closed area, one of the experimental plots was left undredged ("control" plot), whereas the remaining plot was dredged ("dredge" plot). The large size of the plots enabled changes to fish populations within the plots to be monitored using a large trawl net (G.D. Parry and D.R. Currie, unpublished). However, the large size of the plots made replication of control plots (Hulbert 1987; Underwood 1991) prohibitively expensive in all experiments and limited the use of control plots to studies of changes in the abundance of large epifauna and of infauna within the St. Leonards area (Currie and Parry 1996).

Dredge plots were dredged to closely duplicate normal fishing practices, as described in Currie and Parry (1996). Plots were dredged over 2–4 days (Table 1) by a fleet of five to seven commercial scallop vessels using 3-m-wide "Peninsula" dredges (see diagram in Hughes 1973) fitted with scraper or cutter bars that did not extend below the level of the skids. Dredging was conducted for a maximum of 3 h/day and coincided with periods in which tidal currents carried dredging-related sediment away from the control plots. Sediment traps (Black and Parry 1994) placed downcurrent and in the centre and on the southern edge of the control plot at St. Leonards confirmed that negligible sedimentation occurred on the control plot, while sedimentation was greatly elevated downcurrent. At St. Leonards and Dromana, dredge plots were dredged until they had, on average, been passed over twice by a scallop dredge (2× intensity). The dredge plot at Portarlington was dredged twice with an interval of 3 weeks between dredgings of equal (2×) intensity. A 2× intensity of dredging was consistent with a moderately high fishing intensity, based on historical levels in Port Phillip Bay, and a 4× intensity corresponded to very intense dredging (Currie and Parry 1996). A lower level of dredging would also have made detection of impacts more difficult, as much of the dredged plot would have remained undredged. Even at the 2× dredging intensity used in this experiment, an estimated 13% of the plot remained undredged (Currie and Parry 1996).

On each 600-m drag, observers on each vessel recorded the catch of scallops and all bycatch species large enough to be retained by the 70 × 45 mm dredge mesh. Scallops >70 mm were harvested from the catch, and bycatch was discarded on the plot. The numbers of commercial-sized scallops (>70 mm), small scallops (<70 mm), and broken scallops were counted separately. When large numbers of small scallops were caught, only a proportion (0.25 or 0.5) were counted, and when large numbers of oysters were caught the number of fish bins that they filled was recorded. The number of oysters per fish bin was determined subsequently. For oysters and ascidians the number of clumps of live organisms was counted rather than the number of individuals. At Portarlington the number of damaged ascidians and "severely damaged" spider crabs was recorded. Severely damaged spider crabs had their carapace damaged or were missing more than two legs and were considered unlikely to survive. Kaiser and Spencer (1995) found that all crabs taken in trawl nets with cracked carapaces or missing >50% of their limbs died within 48 h.

To assess visually apparent changes caused by dredging, diver-operated video recordings were taken of the seabed on both plots at St. Leonards 3 months before dredging, 8 days after dredging, 6 months after dredging, and 11 months after dredging. At Dromana, video recordings were taken on the dredge plot 1 day before dredging and 5 days after dredging. At Portarlington, poor visibility made it impossible to take video recordings before dredging, but all plots were recorded 43 days, 50 days, 6 months, and 7 months after dredging.

The depth of bed sediment disturbed by dredges was determined using 32–38 sets of colour-coded steel rings that were inserted 2, 4, 6, and 8 cm into the sediment within each dredge plot before dredging commenced. Rings were also placed on the sediment surface, except at St. Leonards. Rings in each set were located within a circle ~50 cm in diameter and sets were placed ~4 m apart (i.e., slightly greater than the width of a dredge) on a line at ~45° to the direction of dredging. During the experimental dredging, observers on each vessel identified each ring and were therefore able to de-

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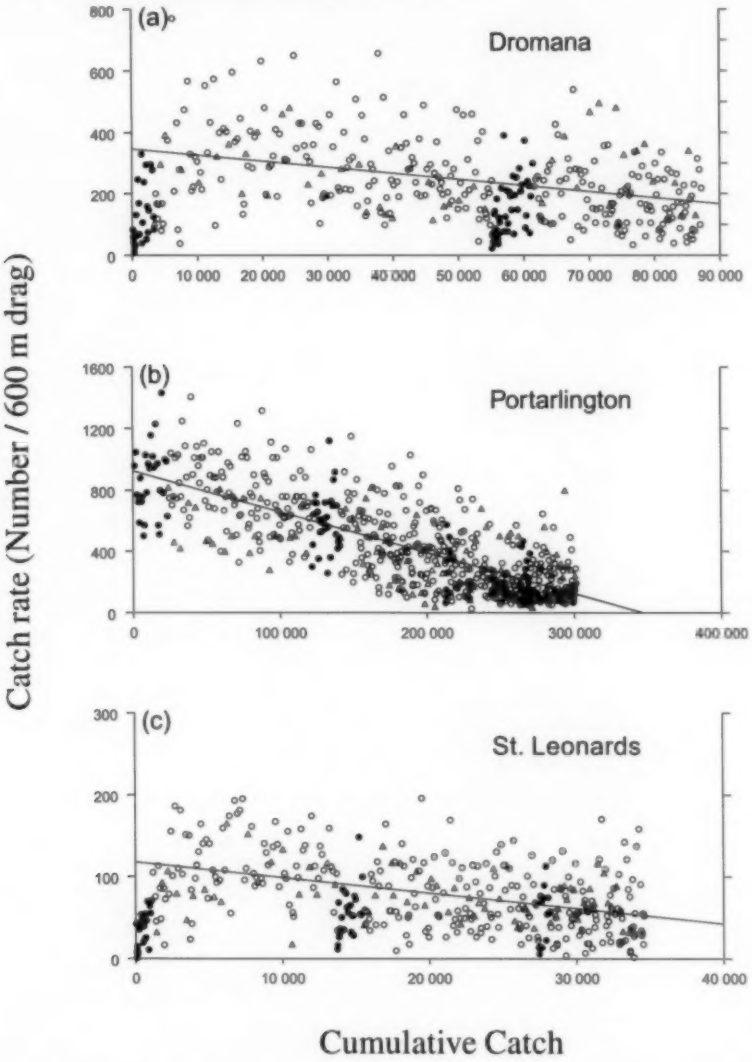
Fig. 2. Leslie–DeLury plots of catch rate against cumulative catch at Dromana, Portarlington, and St. Leonards. The regression lines shown do not include data collected during the first 30 min of dredging each day (●). ○, Catch rates of all vessels other than those (△) for which regressions had a significantly different intercept on the *x*-axis.



termine the depth from which it was recovered (Black and Parry 1994).

Dredge efficiency

A Leslie–DeLury depletion experiment (DeLury 1947; Joll and Penn 1990) was used on each plot to estimate the catch efficiency of dredges for scallops >70 mm. In this method, catch efficiency is estimated from the rate of decline of catch rate compared with the cumulative catch of all vessels (Fig. 2). If the capture efficiency of a fishing gear remains constant, then a fixed fraction of a closed population will be removed with each use of the gear. For example, if a pond is fished four times and the resulting catches are 135, 90, 60, and 40, then the efficiency of the fishing gear will be 1/3 and the initial population size 405. As a scallop dredge only collects scallops in a path the width of the dredge (~3 m) and the plot was 600 m wide, the efficiency of the dredge will be 200 (i.e., 600/3) times the rate of the decline of the population measured in Fig. 2. As the dredge efficiency was constant throughout the dredging on all plots, except during the first 30 min of each day's dredging at Dromana and St. Leonards, catch rates during the first 30 min of each day's dredging were excluded from all estimates of catch efficiency.

The total scallop population on each plot was estimated from the intercept of each regression in Fig. 2 with the *x*-axis. At this intercept the catch rate of all vessels is expected to be zero, so for each vessel the regression of catch rate against cumulative catch should pass through this point. For each vessel the significance of the reduction in sums of squares due to forcing the regression through this point was tested (Steel and Torrie 1960). On each study plot, there was one vessel (shown in Fig. 2) where fitting the regression through the estimated origin significantly increased the sum of squares. Each of these vessels had unexpectedly high catch rates towards the end of each trial and were probably targeting unfished areas near the plot boundaries. Consequently, catch rates for these

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three vessels were then excluded from a recalculated regression of catch rate versus cumulative catch from which another estimate of dredge efficiency was obtained. Differences between the slopes of these recalculated regressions at Dromana, Portarlington, and St. Leonards were tested using analysis of covariance (Snedecor and Cochran 1967).

Mortality of ascidians

To estimate the mortality of ascidians discarded from a scallop dredge, 60 clumps of *Pyura stolonifera* and 60 individuals of *Herdmania momus* were collected from a scallop dredge on 28 October 1992, maintained in flowing seawater for 6 h, and then placed by divers in three marked rows on the seabed near the Dromana plot at a depth of 13–14 m. These ascidians were observed by divers after 7 days and again after 5 weeks and the number of live, dead, and anchored ascidians recorded. Anchored ascidians were those that could not be moved when touched gently by a diver.

Changes in the abundance of large epifauna

Large epifauna was sampled with a 1-m-wide Ockelmann sled towed into the prevailing current for 5 min at 2.2–3.1 kn, except during the preimpact sampling at Portarlington when the sled was inadvertently towed at 3.6–3.8 kn. The duration and the location of the start and finish of each drag were recorded and used to calculate the towing speed and distance of each tow.

In each area, changes in epifauna were assessed using a BACI design where both the control and dredge plots were sampled before and after the experimental dredging. At St. Leonards, epifauna was sampled on three dates before (8 April, 16 May, and 5 July 1991) and on five dates after the experimental dredging (25 July, 9 August, 31 October, and 18 December 1991 and 23 March 1992); on each sampling date, three sled hauls were located randomly on each plot. At Dromana, epifauna was sampled 1 week before (18 August 1991) and twice after the experimental dredging (2 September 1991 and 1 April 1992); nine sled hauls were taken at random within each plot, except on 1 April 1992 when only six hauls per plot were taken. At Portarlington, epifauna was sampled 1 week before the first dredging (14 November 1991), once in the 3 weeks between dredgings (26 November 1991), and twice in the 4 months after the second dredging (12 December 1991 and 2 April 1992); on each sampling date, six sled hauls were located randomly on each plot.

The numbers of large scallops (>70 mm), small scallops (<70 mm), and heart urchins (*Echinocardium cordatum*) caught in each 5-min sled haul were used to estimate the catch of each species per 500 m^2. Differences between the number of individuals per 500 m^2 found on each plot before and after dredging were examined using analysis of variance (ANOVA), as outlined in Underwood (1991, table 1*c*). In these nested ANOVAs, plot × time interactions were tested against the mean square for the plot × date (time) term. Homogeneity of variance was examined using Cochran's test and heterogeneity was removed by a $\log_{10}(N + 1)$ transformation.

Infauna

The distribution and abundance of infauna on each plot were determined from replicate 0.1-m^2 Smith–McIntyre grab samples. All animals retained on a 1.0-mm sieve were sorted to the lowest practical taxonomic level (generally species) under a dissecting microscope before being counted.

At St. Leonards, 15 grabs were taken on both the control and dredge plot on three occasions in the 3 months before and on three occasions in the 3.5 months after the experimental dredging, as described in Currie and Parry (1996). At Dromana, 15 grabs were taken randomly on the dredge plot 8 days before and 2 days after the experimental dredging. At Portarlington, 20 grabs were taken randomly 10 days before the first dredging and 1 day after the second dredging.

Differences in community structure between areas and the effect of dredging on communities in each area were examined using Bray–Curtis (B-C) dissimilarities (Bray and Curtis 1957) and multidimensional scaling (MDS). The PATN computer package (Belbin 1990) was used for the nonmetric MDS ordinations in this study.

There was a pronounced gradient in community structure across both the control and dredge plots at St. Leonards (Currie and Parry 1996). Consequently the eastern third and the western third of these plots were considered as separate "sites". On each sampling date, only the five most easterly and five most westerly grabs taken on the St. Leonards plots were analysed. On each sampling date, plots at Dromana and Portarlington were also subdivided into three and four sites, respectively.The number of individuals of each species on each site was calculated from the total number of individuals found in the five adjacent grabs that formed the site. Before calculating B-C dissimilarities, double square root transformations were applied to the number of individuals of each species. B-C dissimilarity measures calculated for all site × date combinations resulted in a triangular matrix of dissimilarities that was used to map site × date interrelationships in two dimensions.

At Dromana and Portarlington, changes in density on the dredge plots following dredging were examined for the 10 most abundant species using one-way ANOVA's. A $\log_{10}(N + 1)$ transformation removed significant heterogeneity. At Portarlington, many species increased in abundance in the 3-week period between the two experimental dredgings, probably due to recruitment of juveniles. As recruitment obscured dredging impacts on nonrecruits, the size of all animals collected on these plots was measured and size–frequency distributions constructed for periods before and after dredging. Total length was measured for all species except for worms, where head width was used. Measurements accurate to 0.1 mm were made using a camera lucida image projected onto a digitising pad. For each species the largest size class potentially increased by recruitment was estimated and only animals larger than this size (Fig. 3) were included in the ANOVA's. Whilst recruitment was identified in six species, it could only be recognised in species abundant enough for a recruitment mode to be distinguished from size–frequency distributions.

Statistical significance

Results were considered significant if $p < 0.10$. This convention was adopted to reduce the likelihood of making a type II error. Failure to detect a real change due to dredging (type II error) was considered as serious a problem as identifying a change due to dredging when none had occurred (type I error) (Cohen 1988; Peterman 1990; Peterson 1993).

Results

Physical changes to seafloor

At St. Leonards the bedforms were dominated by volcano-like mounds and depressions formed by burrowing callianassid ghost shrimps. Mounds were up to 10 cm high and had an average density of 1.2/m^2 (Currie and Parry 1996), and depressions frequently contained large scallops. Eight days after dredging, ~90% of the seafloor within the dredged plot was very flat, while the remainder appeared undredged. Dredges had a graderlike impact; callianassid mounds were removed and depressions filled, but most callianassids appeared to have survived (Currie and Parry 1996; cf. Peterson 1977) and mounds were being rebuilt. Parallel tracks from the dredge skids (up to 25 mm deep) were obvious. Small scallops remained plentiful and divers estimated that <5% of

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Fig. 3. Size–frequency distributions for six species that recruited between samplings at Portarlington before (open bars) and after dredging (solid bars). The arrowhead indicates the size below which individuals were excluded from ANOVA's for each species.

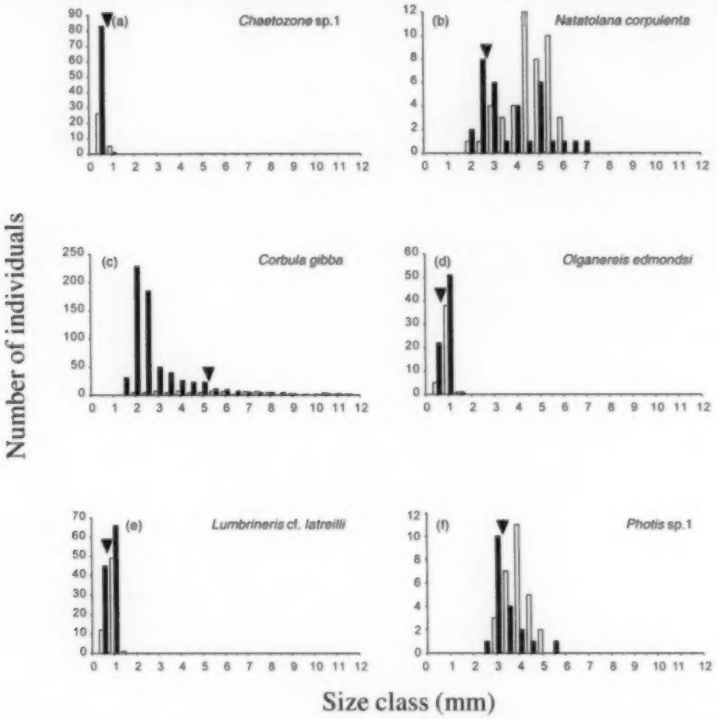

Table 2. Total number of steel rings deployed and recovered from each depth and the number recovered during each day's dredging of experimental plots.

	Depth inserted (cm)														
	Dromana					Portarlington					St. Leonards				
	0	2	4	6	8	0	2	4	6	8	0	2	4	6	8
Total no. of rings deployed	33	33	33	33	33	38	38	38	38	38	0	32	32	32	32
No. of rings recovered on day 1	7	1	1	0	0	0	0	0	0	0	—	0	0	0	0
No. of rings recovered on day 2	1	0	0	0	0	1	0	0	0	0	—	1	0	1	0
No. of rings recovered on day 3	—	—	—	—	—	0	0	0	0	0	—	5	2	0	0
No. of rings recovered on day 4	—	—	—	—	—	1	1	1	0	0	—	—	—	—	—
Total no. of rings recovered	8	1	1	0	0	2	1	1	0	0	—	6	2	1	0

the remaining scallops were dead. One month after dredging, the seabed remained flat and dredge tracks could still be distinguished. Six months after dredging, tracks could no longer be seen, and while mounds and depressions had reestablished, the regions between them remained unusually flat. After 11 months the appearance of the dredged plot could not be distinguished from that of the undredged plot.

At Dromana the seabed consisted of sandy sediments containing some coarse shell. Small parallel sand ripples were evident in parts of the plot, but throughout the plots the bottom relief was mostly the result of callianassid mounds, but these were smaller than and less abundant than in the plots off St. Leonards. Five days after the experimental dredging, and immediately following a period of storm activity, the seafloor was dominated by small parallel sand ripples. Storms had apparently reworked the sediments into sand ripples, obliterating the predredging bedforms and any signs of tracks from dredge skids. Divers estimated that 20% of the remaining scallops were dead.

At Portarlington the dredge plot was initially very flat, except for small numbers of callianassid mounds. Mounds were flattened by dredging, and although they became reestablished, they were still smaller than in adjacent undredged areas 7 months later.

The recovery rate of rings was low on all areas (Table 2), but particularly at Portarlington. The maximum depth of disturbance was 4 cm at Dromana and Portarlington and 6 cm at St. Leonards (Black and Parry 1994).

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Table 3. Regression equations of catch rate against cumulative catch from Leslie–DeLury depletion experiments (Fig. 2) and the initial scallop density and dredge efficiency *a*, derived from these equations, and dredge efficiency *b*, estimated after excluding vessels where the intercept on the *x*-axis for that vessel differed significantly from the overall intercept.

Plot	Gradient	±SE	Intercept	Initial scallop density (no./m^2)	Mean dredge width (m)	Dredge efficiency *a*	±SE	Dredge efficiency *b*
Dromana	–0.00200	0.00026	347.2	0.48	3.17	37.9	4.9	43.9
Portarlington	–0.00268	0.00010	927.1	0.96	3.14	51.2	1.9	55.6
St. Leonards	–0.00187	0.00020	117.7	0.18	3.12	45.0	4.8	49.5

Table 4. Percentage of severely damaged spider crabs (*Leptomithrax gaimardii*) and damaged ascidians (*Pyura stolonifera* and *Cnemidocarpa etheridgii*) found in scallop dredges during each day of experimental dredging at Portarlington.

Date	*Leptomithrax gaimardii*	*Pyura stolonifera*	*Cnemidocarpa etheridgii*
20 Nov. 1991	36	1.4	2.7
21 Nov. 1991	54	0.6	0.5
10 Dec. 1991	22	0.6	0.2
11 Dec. 1991	55	0.9	0.3

Dredge efficiency

Dredge efficiencies differed between experimental plots. These differences were of marginal significance: $p = 0.07$ for analysis of heterogeneity of slopes of regression lines in Fig. 2. Dredges were most efficient on the soft, muddy, and flat Portarlington plot (51–56%, Table 3) and least efficient on the firm, sandy, and moderately flat Dromana plot (38–44%). However, dredge efficiencies during the first 30 min of dredging differed markedly between areas (Fig. 2). At St. Leonards and Dromana the efficiency of dredging increased during the first 30 min of fishing on each day, and this was particularly marked on the first day (Fig. 2). In contrast, at Portarlington, dredges always operated at their maximum efficiency from the commencement of each day's fishing.

Effect on larger epifauna

Dredge catches

There were clear differences in the bycatch between areas (Table 1). Oysters (*Ostrea angasi*), sea squirts (*Herdmania momus*), giant spider crabs (*Leptomithrax gaimardi*), whelks (*Austrosipho grandis*), and hermit crabs were collected most frequently in the sandy sediments at Dromana. In the muddy sediments at Portarlington, sea squirts (*Pyura stolonifera* and *Cnemidocarpa etheridgii*), sea cucumbers (*Stichopus mollis*), biscuit stars (*Tosia magnifica*), and octopus (*Octopus australis* and *Octopus pallidus*) were the dominant species of bycatch. At St. Leonards, bycatch included species taken at both Dromana and Portarlington.

Dredges caught mostly scallops. The total number of nonbivalve epibiota (TNBE) caught was typically <5% of the number of commercial-sized scallops caught (Table 1). The highest percentage of TNBE/scallops >70 mm was 10.6% at Portarlington but occurred only after 4 days of dredging, when most of the scallops had been caught. Catches of scallops <70 mm were high at all areas, and many oysters were caught at Dromana (Table 1).

Damage and mortality caused by dredging

Less than 1% of scallops taken in dredges were damaged (Table 1). The percentage of damaged scallops was higher at Dromana (0.75–1.0%) than at Portarlington (0.11–0.38%) and St. Leonards (0.22–0.45%), but it is likely that some damaged scallops were overlooked by observers.

Damaged oysters were not counted, but they were observed only rarely and their shells are more robust than those of scallops. At Portarlington, slightly more than half the spider crabs (up to 55%, Table 4) were probably killed by dredges, and a similar percentage of the many spider crabs caught at Dromana (Table 1) was also damaged (personal observations). The percentage of ascidians damaged at Portarlington (0.2–2.7%, Table 4) was low, and while the proportion damaged was probably higher in firmer sediments at Dromana, the number of conspicuously damaged ascidians was always low.

Although most oysters and ascidians were not physically damaged by dredges, their survival after they are discarded also depends on their orientation on the seafloor and their ability to reanchor themselves in the sediment. Trials to measure survival of ascidians caught by scallop dredges and returned to the sea by divers showed nearly 100% survival of *Herdmania momus* and *Pyura stolonifera* in the week following their return, but storms during the following 5 weeks moved most of the experimental animals out of the study area (Table 5) and they could not be relocated. Only 12% of *Pyura stolonifera* and 2% of *Herdmania momus* successfully reanchored on our experimental area after 6 weeks. *Herdmania momus* is more globular in shape than *Pyura stolonifera* and seems less able to reanchor itself. Fewer than 7% of the experimental ascidians were known to have died, and the proportion that reanchored elsewhere was unknown, but most of them probably died.

Changes to epifauna

The abundance of small (<70 mm) scallops decreased significantly ($p < 0.10$) by 57% in the 7 months following dredging at Dromana and by 26% in the 5 months following the first dredging at Portarlington, but increased significantly by 19% in the 8 months following dredging at St. Leonards (Table 6). At Dromana and Portarlington, both large scallops (>70 mm) and heart urchins decreased in abundance, but these changes were not significant, while at St. Leonards, their abundance increased, but not significantly (Table 6).

Infauna

Differences between infaunal communities

An MDS plot (Fig. 4) indicated that all sites sampled at Dromana and Portarlington and the eastern and western sides

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Table 5. Percentage of live, anchored, and dead ascidians on an experimental plot 1 and 5 weeks after 60 clumps of two species of ascidians were caught in a scallop dredge and placed on the seabed.

	Pyura stolonifera			*Herdmania momus*		
No. of weeks after dredging	Live	Anchored	Dead	Live	Anchored	Dead
1	100.0	38.3	0	66.7	20.0	3.3
5	41.7	11.7	6.7	1.7	1.7	0

Table 6. Mean densities on control plots, mean difference between dredge and control plots, and percentage change following dredging in the abundance of common fauna collected by Ockelmann sled at Dromana, Portarlington, and St. Leonards.

		Mean densities (SE) on control plot/500 m^2		Mean % difference dredge vs. control		
Site	Taxa	Before dredging	After dredging	Before dredging	After dredging	% change
Dromana	Scallops ≥70 mm	4.1 (0.7)	16.0 (3.6)	–13.4	–79.4	–66.0
	Scallops <70 mm	63.3 (7.9)	125.1 (29.4)	+13.8	–43.1	–56.9*
	Heart urchins	2.0 (0.8)	32.4 (9.9)	+338.8	+45.2	–293.6
Portarlington	Scallops ≥70 mm	21.9 (3.6)	33.3 (5.0)	+33.2	–28.6	–61.8
	Scallops <70 mm	81.8 (19.1)	179.8 (29.8)	+3.9	–22.3	–26.2*
	Heart urchins	0.6 (0.3)	7.2 (2.5)	–1.8	–54.6	–52.8
St. Leonards	Scallops ≥70 mm	2.4 (1.0)	4.6 (1.8)	–76.7	–49.4	+27.3
	Scallops <70 mm	50.6 (12.1)	57.8 (9.4)	–23.6	–5.1	+18.5*
	Heart urchins	36.9 (13.2)	46.8 (15.6)	+18.2	+37.1	+18.9

Note: *$p < 0.1$.

of the St. Leonards plot formed separate clusters. The stress value of 0.127 indicates that the pattern is unlikely to mislead (Clarke 1993). The most similar plots were west St. Leonards and Dromana, both of which occurred in sandy sediments (1–24% sediment <63 μm) and both of which had a high diversity of species. The east St. Leonards plot had a lower diversity of species and lower numbers of individuals and was muddier than the west (Currie and Parry 1996). The Portarlington plot was the muddiest (15–55% sediment <63 μm) and had the lowest diversity of species and the lowest number of individuals. Sites sampled before and after dredging within the same plot did not form separate clusters (Fig. 4), indicating that changes to community structure caused by dredging were smaller than differences between plots.

Changes to infauna

Three of the 10 most abundant species at Dromana (*Bullowanthura pambula*, *Chaetozone* sp.1, and *Nephtys inornata*) decreased significantly in abundance by 20–40% (Table 7). The abundance of *Bullowanthura pambula* decreased at all areas following dredging, although the significant "decrease" at St. Leonards appeared to be caused by aggregation of this motile paranthurid in undredged regions immediately following dredging (Currie and Parry 1996). *Chaetozone* sp.1 was rare at Portarlington but appeared to decrease by 30–40% at both Dromana and St. Leonards (Table 7). The decrease in abundance of *Nephtys inornata* may be greater at Dromana than at St. Leonards (Table 7).

Two of the 10 most abundant species at Portarlington (*Theora lubrica* and *Natatolana corpulenta*) decreased significantly in numerical abundance by 30–70%, although these changes should be interpreted cautiously, as densities of all species at Portarlington were low (Table 7). Changes to the abundance of *Theora lubrica* are not considered reliable, as this species has a very patchy distribution (Currie and Parry 1996). The decrease in the abundance of *Natatolana corpulenta* is similar to its sharp decrease immediately following dredging on the St. Leonards plot but contrasts with its apparent increase on the St. Leonards plot in the months following dredging (Currie and Parry 1996)

Discussion

Physical differences between the experimental plots at Dromana, St. Leonards, and Portarlington affect the impact of dredges and their efficiency. Dredging removed most topographic variation from all plots and caused the most noticeable changes at St. Leonards where callianassid mounds were a prominent predredging feature. Recovery of rings and measurements of sediment concentrations behind dredges (Black and Parry 1994) suggest that dredges usually disturb less than the top 1–2 cm of sediment, although they can clearly disturb up to at least 6 cm. Plume modelling suggests that on average, ~0.5 cm of sediment was disturbed in all areas (Black and Parry 1999).

Our estimates of the efficiency of Peninsula dredges in Port Phillip Bay (38–56%, Table 3) were similar to other estimates obtained in Port Phillip Bay (42–66%, McShane and Gwyther 1984; 37–50%, Gwyther and Burgess 1986) but were markedly higher than the 12% measured experimentally in Bass Strait (McLoughlin et al. 1991). We observed the lowest efficiency on the hardest substrate (Dromana, Table 3) most like the sediments in Bass Strait, but the very low efficiency found by McLoughlin et al. (1991) was probably due to the small number of drags (~20) undertaken in their study. We found that dredge efficiencies were markedly lower during the first 30 min (~20 drags) of dredging on

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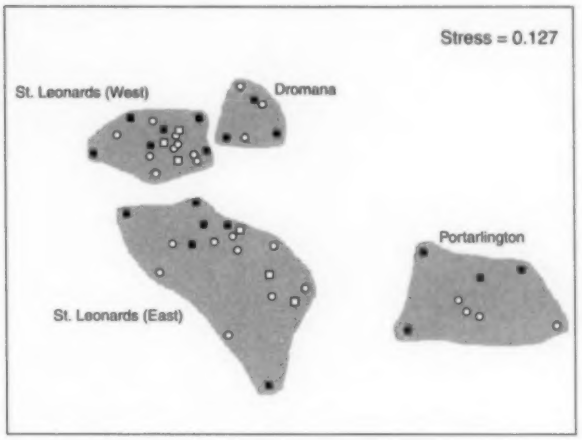
Fig. 4. MDS ordination of benthic community data based on five pooled grab samples taken from study plots on sampling dates before and after dredging. ○, Dredge plot before dredging and (St. Leonards only) control plot before and after dredging; ■, dredge plot after dredging; □, dredge plot before dredging (St. Leonards only).



both plots with sandy substrates. Higher vessel speeds used in our study (5.5–6.5 versus 2–3 kn) and the use of toothbars only in Bass Strait may also have contributed to differences between the studies.

Increases in dredge efficiency observed during the first 30 min of dredging on two of our three experimental plots appear similar to increases noticed by commercial scallop fishers as they "worked up" scallops. Differences in dredge efficiency between areas and the observation that sediment plumes usually cause scallops to swim suggest an explanation for this phenomenon. On soft flat substrates (e.g., Portarlington) all scallops are similarly likely to be caught by a passing dredge. In contrast, on substrates with greater topographic relief (e.g., Dromana and particularly St. Leonards), most large scallops occur in depressions where they may be passed over by a dredge. However, the sediment plume thrown up by a passing dredge stimulates many scallops to swim and they become more randomly distributed and more vulnerable to dredges that pass subsequently. As dredging continues the substrate is progressively flattened, so fewer scallops remain in depressions deep enough to be passed over by a dredge. The increasing flatness of the plots at Dromana and St. Leonards on the second and third days of dredging probably caused the progressively higher efficiencies observed at the commencement of dredging on successive days (Fig. 2). Levelling of the previously uneven substrate on the St. Leonards plot was also consistent with postdredging increases in the efficiency of the Ockelmann sled (Table 6) and a fish trawl net (G.D. Parry and D.R. Currie, in preparation) that occurred only on this plot. The increase in dredge efficiency from a more rapid increase in turbidity and a more rapid levelling of the substrate when several vessels operate in the same area probably explains why scallop vessels usually operate in groups.

The proportion of scallops damaged by dredging was consistently low but was highest at Dromana (Table 1), where the relatively firm sediments probably increased the forces on scallops trapped beneath the passing dredge skids. These firmer sediments may also cause dredges to bounce more, further increasing the likelihood of damage to scallops. Divers also observed the highest percentage (20%) of dead scallops on the Dromana plot after it was dredged, and mortality estimates of small scallops, based on catches in an Ockelmann sled, were also highest at Dromana (57% in 7 months, Table 6). However, estimates of scallop mortality at Portarlington and St. Leonards may be unreliable. At Portarlington, all epifaunal abundances were underestimated predredging due to excessive towing speed, whereas at St. Leonards the increased catches of all species after dredging (Table 6) appear to be an artefact caused by an increase in the efficiency of the Ockelmann sled after dredging flattened the plot. The proportion of damaged scallops even at Dromana (~5%, Table 1) was much lower than was observed on an intensively fished, very dense bed of scallops in Bass Strait where over 40% of scallops taken in dredges were damaged (McLoughlin et al. 1991).

Scallop dredges caught mostly scallops (Table 1) because scallops are the dominant epifaunal species in the main scallop grounds in Port Phillip Bay. The main bycatch species taken in dredges were oysters, ascidians, and, periodically, spider crabs. Survival of discarded epifauna requires further investigation, but mortality rates of oysters were probably low, while those of ascidians were probably high (Table 5) and those of spider crabs were high (>50%, Table 4). The ecological consequences of the removal of spider crabs are uncertain, but as their populations remain large, despite being dredged for 30 years, their survival cannot be threatened seriously by scallop dredging.

At St. Leonards, infauna was typically reduced in abundance by 20–30% in the 3.5 months following dredging (Table 7; Currie and Parry 1996). Changes caused by dredging at Dromana and Portarlington were similar to those at St. Leonards despite the much higher intensity of dredging at Portarlington. However, few changes in abundance measured at Dromana and Portarlington were significant because sampling was inadequate to detect changes comparable with those observed at St. Leonards (power of test, Table 7). Kaiser and Spencer (1996) found that trawling reduced infauna by up to 58% but that effects were undetectable in more mobile sediments. The BACI design used at St. Leonards (Currie and Parry 1996) provides a robust measure of fishing impacts on infauna. The absence of spatial control plots at Dromana and Portarlington in this study and of before/after temporal controls in Kaiser and Spencer's (1996) studies means that unmeasured temporal or spatial variation may have influenced the results of these studies.

Infaunal communities on our study plots were similar to the "intermediate sediment" community found in the main scallop grounds in Port Phillip Bay (Fig. 1*b*; Currie and Parry 1999). Scallop dredging also occurred on other infaunal communities in coarser and finer sediments. Dredging impacts are only likely to be greater than measured on our plots in the finer sediments in the centre of the bay. These sediments are seldom disturbed by natural storms (De Groot 1984; Theil and Schriever 1990; Jones 1992; Kaiser and Spencer 1996), and their infaunal communities may be more sensitive to the short-lived but very large increases in sedi-

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Table 7. Percentage change following dredging, predredging abundance, and power of ANOVA's to detect 30 and 50% change following dredging for the 10 most abundant species at Dromana, Portarlington, and St. Leonards.

						Power of test (p = 0.05)			
	Percentage change following dredging			Predredging abundance(no./0.1 m^2)		Dromana		Portarlington	
Species	Dromana	Portarlington	St. Leonards	Dromana	Portarlington	Δ30%	Δ50%	Δ30%	Δ50%
Aricidea sp. 1	152		–26	3.5		0.15	0.43		
Artacamella dibranchiata	3	–23	–28**	21.9	3.1	0.12	0.34	0.24	0.69
Bullowanthura pambula	–28**	–16	–0.4**	17.9	2.3			0.35	0.87
Byblis mildura	–28		13	5.0		0.26	0.73		
Corbula gibba	14		–66**	21.3		0.16	0.46		
Dimorphostylis cottoni	28	–49	119	13.9	6.8	0.47	0.96	0.17	0.49
Lumbrineris cf. *latreilli*	8		–18	19.5		0.30	0.80		
Nephtys inornata	–21*		–3	20.3					
Photis sp. 1	14		–79**	10.5		0.17	0.48		
Prionospio coorilla	3		–60	46.5		0.16	0.46		
Ampharete sp. 1	–35			8.7		0.28	0.76		
Chaetozone sp.1	–38**		–32	11.0					
Asychis sp. 1		11			7.7			0.72	0.99
Marphysa sp. 1		–12			4.9			0.62	0.99
Natatolana corpulenta	–39*	–66**	23	3.1	2.1				
Theora lubrica		–29*			3.6				

Note: At St. Leonards, percentage change is that during 3.5 months following dredging (Currie and Parry 1996). Data are shown only for species with densities >2.0/0.1 m^2. *p < 0.1, **p < 0.05.

mentation rates that occur behind scallop dredges (Black and Parry 1994).

Adequate data on the abundance of epifauna in Port Phillip Bay before dredging commenced do not exist. Anecdotal information suggests that dredging may have levelled low-relief inshore reefs on the east of the bay and severely damaged some seagrass communities on the west of the bay before dredging in these shallow regions was prohibited in 1985. But in the main scallop grounds, where epibiota other than scallops is uncommon, changes to infauna are small enough to be difficult to detect without a large and expensive sampling program. Results of this study and Currie and Parry (1996) are consistent with an emerging generalisation that the effects of fishing gear dragged along the seafloor depend largely on the amount of epibiota in the area being trawled or dredged. Impacts are large where epifauna and epiflora (e.g., bryozoans, tube-building polychaetes, sponges, and seagrass) form a habitat that is itself vulnerable to fishing gear because it is fragile, inflexible, easily uprooted, or large enough to be retained by the gear (Bradstock and Gordon 1983; Peterson et al. 1987; Sainsbury 1988; Collie et al. 1997). The extent of impacts will also depend on the frequency of disturbance and the recovery rate of the biota (Van Dolah et al. 1987; Hall 1994).

Changes to infauna caused by scallop dredging are smaller than the cumulative changes to community structure of infauna in Port Phillip Bay over the past 20 years (Currie and Parry 1999). The contribution of 30 years of scallop dredging to these ecological changes is unclear. Like many bays with urbanised catchments, there are many possible causes of long-term change. Over 20 years, there has been an increase in nutrient loads, increasing algal blooms (Parry et al. 1989), the introduction of several new exotic species (Currie and Parry 1999), decreased discharge of most toxicants (Fabris et al. 1992; Phillips et al. 1992) but an increase in tributyl tin (Foale 1993), and increasing fishing pressure (Hobday et al. 1999). In addition, natural temporal changes in community structure may be contributing, although they remain unmeasured.

Scallop dredging may be the main cause of the marked decrease in size and longevity of scallops in Port Phillip Bay over this same period. Few scallops now live beyond 3 years or 75 mm, when they once lived to an age of 7 years and the minimum legal size during the early years of the fishery was 80 mm (Gwyther and McShane 1988). Scallops of this size have not been seen for many years, even in lightly fished areas, suggesting that factors other than fishing mortality may be important. A large bloom of the toxic diatom *Rhizosolenia chunii* caused widespread mortality in 1988 (Parry et al. 1989), resulting in the closure of the fishery in 1989 and 1990. Blooms of *Rhizosolenia chunii* have been recorded in 1975, 1987 (Parry et al. 1989), 1993, 1994, and 1997 (G. Arnott, Marine and Freshwater Resources Institute, Queenscliff, personal communication), and their frequency appears to be increasing. In 1992 and 1993, very large recruitments (1+ age class) made only minor contributions to increased

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fishing yields, as mortality rates were very high and many died while the fishery was closed over summer (N. Coleman, Marine and Freshwater Resources Institute, Queenscliff, personal communication). It is also of concern that there have been no commercial quantities of scallops in central Port Phillip Bay since the virgin stock was eliminated in the 1960's. However, the failure of scallop populations to reestablish in the centre of the bay may be unrelated to dredging. Since the 1970's the European bivalve *Corbula gibba* has been introduced into Port Phillip Bay where it now occurs in densities of 1000/m^2 at St. Leonards (= *Corbula* cf. *coxi*, Currie and Parry 1996), and competition for food between scallops and *Corbula gibba* is likely, particularly in muddier regions in the centre of the bay where *Corbula gibba* is abundant (Parry et al. 1995).

Most community concern with scallop dredging and other potential impacts is with their possible long-term effects. The recent, and apparently permanent, closure of the scallop fishery in Port Phillip Bay provides an opportunity to determine more confidently the contribution of scallop dredging to long-term changes. Studies are now in progress to monitor the recovery of Port Phillip Bay, but as dredging is only one of many potential impacts causing ecological changes on time scales of decades, it is important that dredging impacts are maintained in small areas within the "recovering" community so that the role of dredging itself can be identified. Ironically, two of the species most impacted by scallop dredging are recently introduced species, the bivalve *Corbula gibba* (Currie and Parry 1996) and the large epifaunal sabellid polychaete *Sabella spallanzanii* (G.D. Parry, personal observations), and cessation of dredging may increase their ecological effects.

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Estimation and effects of tag-misread rates in capture–recapture studies

Carl James Schwarz and Wayne T. Stobo

Abstract: Virtually all capture–recapture studies assume that tags are read properly when an animal is captured. However, the animals in resighting studies are often not handled, tags are read at a distance, and misreads can occur. In this paper, we develop a simple model to account for misreads, assess the impact of misreads upon estimates of survival and catchability, and analyze a set of data from resightings of previously branded seals. In general, unless survival, capture, and misread rates are relatively high, most studies have poor power to detect misreads and estimates of survival are not severely biased. Estimates of capture rates will be biased downwards and will tend to estimate the product of the original capture rate and the complement of the misread rate.

Résumé : Dans presque toutes les études de marquage–recapture, on assume que les marques sont lues correctement quand un animal est recapturé. Cependant, dans les études de marquage–observation, les animaux marqués ne sont généralement pas manipulés, les marques sont lues à une certaine distance et les lectures peuvent être erronées. Dans cet article, nous présentons un modèle simple permettant de tenir compte des lectures erronées, évaluons l'impact des lectures erronées sur les estimations de la survie et de la capturabilité et analysons un ensemble de données sur des observations de phoques marqués visuellement. En général, à moins que les taux de survie, de capture et de lectures erronées soient relativement élevés, on réussit mal à détecter les lectures erronées dans la plupart des études, et les estimations de la survie ne sont pas gravement biaisées. Il y aura sous-estimation des taux de capture et on tendra à estimer le produit du taux de capture original par la probabilité que les marques soient lues correctement.

[Traduit par la Rédaction]

Introduction

One of the assumptions made for capture–recapture studies is that tag numbers are read without error whenever an animal is captured. Surprisingly, the effect of tag misreads and how to estimate the misread rate have not been previously considered.

Errors in reading tag numbers is a particular problem in "resighting studies" where the animal is not physically handled. For example, the context of this paper is a mark–resight study of seals branded as pups and resighted as adults several years later where the subsequent "recaptures" are sightings taken from a distance. The brand may be partially covered with sand, the animals may be moving when sighted, the weather conditions may impede a clear reading of the brand number, or the brand was poorly applied resulting in portions of the brand being indistinct. Other contexts in which misreads may be a problem are where tag numbers deteriorate over time (e.g., ring colors fading over time or rings cracking and pieces breaking off), where untrained personnel (e.g., volunteers in a bird survey) are used to spot and record tag numbers, or where animals are "self-marking" (e.g., whales identified through scars and other markings).

In this paper, we develop a very simple model for misread errors, investigate the general effect of misreads upon the estimates when the usual models ignoring the problem of misreads are applied, and then apply our methodology to a resighting study of previously branded seal pups.

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Methods

Statistical notation

Assume that there are K sample times and, for simplicity, that there are neither losses on capture nor injections at any sample time. We consider a single cohort released at time 1 of a known size, in which each animal is tagged with a unique tag number. This is the usual setup for a Cormack–Jolly–Seber (CJS) study (Cormack 1964; Jolly 1965; Seber 1965).

A total of $R_1 = N_1$ animals are originally captured, tagged, and released with individual tag numbers $1,\ldots, N_1$. In actual practice, tag numbers may be codes of letters, numbers, symbols, colors, etc., but for this paper, we will assume that they are sequentially numbered. When misreads are possible, there is no longer a one-to-one correspondence between observing a particular tag number and observing the particular animal originally tagged with that tag number. We will use the terms "observing a tag number" and "capturing an animal", respectively, to distinguish between the two events.

Parameters

- ϕ_i probability that an animal alive at time i will be alive and in the population at time $i + 1$; permanent emigration is indistinguishable from and confounded with death
- p_i probability that an animal alive at time i will be captured; this differs from the usual definition in capture–recapture studies

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in that we do not assume that the tag number will be read correctly

θ_i probability that an animal captured at time i will have its tag correctly read

ν_i probability that if a tag is incorrectly read at time i, then it is observed as a valid tag number

p_i^{misread} probability that the tag number for a particular animal will be observed at time i through a misread of some other captured animal

p_i^{alive} probability that the tag number for a particular animal will be observed if the animal is alive at time i; this could occur through an animal being captured and its tag being read properly or from a misread from another animal captured

p_i^{dead} probability that the tag number for a particular animal will be observed if the animal is dead at time i; this can only occur through a misread of a tag number for another animal captured at the same time

λ_i^{alive} probability that a tag number corresponding to a particular animal alive at time i will be observed after time i

λ_i^{dead} probability that a tag number corresponding to a particular animal dead at time i will be observed after time i

N_i number of animals (out of those released) that are alive at time i; N_1 is known; $E[N_i] = N_1\phi_1\ \phi_2, \ldots, \phi_{i-1}$

Statistics

$\mathbf{h} = (h_1, h_2, \ldots, h_K)$ generic encounter history vector for a particular tag number where $h_i = 1$ if the tag number is observed at time i and $h_i = 0$ if the tag number is not observed at time i; because all animals were released alive at time 1, $h_1 = 1$ for all animals

$n_{\mathbf{h}}$ number of tag numbers with capture history h; this is distinguished from n_i (below) by the context in which it is used

$R_i = n_i = m_i$ number of tag numbers observed at time i; in the CJS model, all recaptures are of previous marked animals, and so, $m_i = n_i$; if there are no losses on capture, the number of tag numbers released is equal to the number of tag numbers observed (in our example, recaptures are resightings and so there are no losses)

r_i number of tag numbers recovered (in the sense that the tag number is again observed) out of R_i after time i

z_i number of tag numbers observed before time i, not observed at time i, and observed after time i

Matrices

$\boldsymbol{\Phi}_i$ 2×2 matrix with elements $\begin{bmatrix} \phi_i & 1-\phi_i \\ 0 & 1 \end{bmatrix}$

$\mathbf{p}_i$ 2×1 matrix with elements $\begin{bmatrix} p_i^{\text{alive}} \\ p_i^{\text{dead}} \end{bmatrix}$

$\mathbf{D}(\cdot)$ operator that makes a matrix with zeroes on the off-diagonals and its vector argument along the main diagonal

Statistical model and its assumptions

We will assume that a standard CJS study (Cormack 1964; Jolly 1965; Seber 1965) is being conducted on a single cohort of animals and will make the usual assumptions.

At the end of the study, each tag number will have a capture history $\mathbf{h} = (h_1, h_2, \ldots, h_K)$. For example, if $K = 4$, the history vector $\mathbf{h} = (1, 0, 1, 1)$ corresponds to this tag number being observed at time 1 (its release) and times 3 and 4. The actual capture history of the corresponding animal may be different because of misreads. For example, the event $h_3 = 1$ can occur either because the corresponding animal was alive, captured at time i, and its tag read properly or some other animal was captured, its tag misread, and the misread generated this tag number.

Note that in some cases, misreads will generate tag numbers that are not possible, e.g., a number never applied. If these are recorded, this information will give a lower bound on the tag misread rate.

The major difficulty in computing the probability of a particular history vector (which is needed in order to construct the likelihood function) is the modelling of the misread process.

We will assume that if a misread occurs, then any one of the $N_1 = R_1$ initial tag numbers is equally likely to be generated. However, the chance that a tag number is misread and the value of the subsequent misread in real life is not equal for all tags and depends upon many factors such as the way the tag is applied to animals, the conditions under which it is read, the particular set of tag numbers used, etc. For example, in our seal study, the brand numbers are observed at a distance of 2–4 m and individual digits may be partially obscured by dirt or shade or be indistinct due to poor brand application. Under these circumstances, the digit "7" is more likely to be misread as a "1" rather than an "8". Nevertheless, our simple model appears to work well, as illustrated in our example later in the paper.

Under this assumption, we can derive a simple expression for the probability that a tag number will be observed through a misread. At sample time i, there are N_i animals alive. Each of these has a probability of p_i of being captured, a probability of $(1 - \theta_i)$ that a misread will occur, a probability of ν_i that the misread will generate a legitimate tag number, and a probability of $1/N_1$ that a particular tag number will be generated through the misread. Consequently, there is a probability of $1 - p_i(1 - \theta_i)\nu_i \frac{1}{N_1}$ that a particular tag number will *not* be generated by a misread of another animal's tag. However, this nonevent must occur for every one of the N_i animals alive, and so the probability that a particular tag number will be observed at time i because of a misread is

$$p_i^{\text{misread}} = 1 - \left[1 - p_i(1-\theta_i)\nu_i \frac{1}{N_1}\right]^{N_i}$$

$$\approx p_i(1-\theta_i)\nu_i \frac{N_i}{N_1}$$

$$\approx \phi_1\phi_2, \ldots, \phi_{i-1}p_i(1-\theta_i)\nu_i$$

which does not depend upon the number of animals originally tagged or upon the number of animals currently alive at time i (except indirectly through the survival rates).

The p_i^{misread} can be used to derive the conditional probabilities of observing an animal's tag number at time i if it is dead, p_i^{dead}, or if it is alive, p_i^{alive}. A dead animal's tag number can only be observed through a misread, hence, $p_i^{\text{dead}} = p_i^{\text{misread}}$. On the other hand, an alive animal's tag number can be observed either because it is captured and the tag is read properly or because a misread of another animal occurs. Because these two possibilities occur independently:

$$p_i^{\text{alive}} = p_i\theta_i + p_i^{\text{misread}} - p_i\theta_i p_i^{\text{misread}}$$
$$= 1 - [1 - p_i\theta_i][1 - p_i^{\text{misread}}].$$

Finally, the probability of the entire history vector is found by examining all the possible (unknown) survival and capture processes that could lead to the observed capture history vector. For example, the history vector $\mathbf{h} = (1, 0, 1, 1)$ could have occurred by the animal surviving until time 4 with the observed h_i depending only upon the p_i^{alive}, or the animal may have died at sample time 3, and the final observation is a misread from another animal, etc. In this case, there are four possible survival and capture processes

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that could lead to the observed history, and the overall probability of the history is found as

$$\begin{aligned}P(\mathbf{h}=(1,0,1,1)) &= \phi_1(1-p_2^{\text{alive}})\phi_2 p_3^{\text{alive}}\phi_3 p_4^{\text{alive}} \\ &+ \phi_1(1-p_2^{\text{alive}})\phi_2 p_3^{\text{alive}}(1-\phi_3)p_4^{\text{dead}} \\ &+ \phi_1(1-p_2^{\text{alive}})(1-\phi_2)p_3^{\text{dead}}p_4^{\text{dead}} \\ &+ (1-\phi_1)(1-p_2^{\text{dead}})p_3^{\text{dead}}p_4^{\text{dead}}.\end{aligned}$$

It is the potential for misreads to generate observations of a particular tag number when the animal has died that makes the construction of the likelihood for a particular capture history vector extremely complex. However, it can be greatly simplified by recasting the problem as a multistratum framework, as suggested by Lebreton et al. (1998). In this problem, there are two strata (alive or dead) in which an animal can be present at time i with a transition matrix $\boldsymbol{\phi}_i$ for the probability of changing strata between time i and time $i + 1$. Using a similar argument as used in Brownie et al. (1993) and Schwarz et al. (1993), the probability of history $\mathbf{h}$ for a particular tag number can be found as

$$\begin{aligned}P(\mathbf{h}) = &\begin{bmatrix}1\\0\end{bmatrix}^t \times \boldsymbol{\phi}_1 \times \begin{Bmatrix}\mathbf{D}(\mathbf{p}_2) & \text{if } h_2 = 1\\ \mathbf{I}-\mathbf{D}(\mathbf{p}_2) & \text{if } h_2 = 0\end{Bmatrix} \\ &\times \boldsymbol{\phi}_2 \times \begin{Bmatrix}\mathbf{D}(\mathbf{p}_3) & \text{if } h_3 = 1\\ \mathbf{I}-\mathbf{D}(\mathbf{p}_3) & \text{if } h_3 = 0\end{Bmatrix} \times \cdots \\ &\times \boldsymbol{\phi}_{K-1} \times \begin{Bmatrix}\mathbf{D}(\mathbf{p}_K) & \text{if } h_K = 1\\ \mathbf{I}-\mathbf{D}(\mathbf{p}_K) & \text{if } h_K = 0\end{Bmatrix} \times \begin{bmatrix}1\\1\end{bmatrix}.\end{aligned}$$

For example:

$$\begin{aligned}P(\mathbf{h}=(1,0,1,1)) = &\begin{bmatrix}1\\0\end{bmatrix}^t \times \begin{bmatrix}\phi_1 & 1-\phi_1\\ 0 & 1\end{bmatrix} \\ &\times \begin{bmatrix}1-p_2^{\text{alive}} & 0\\ 0 & 1-p_2^{\text{alive}}\end{bmatrix} \\ &\times \begin{bmatrix}\phi_2 & 1-\phi_2\\ 0 & 1\end{bmatrix} \times \begin{bmatrix}p_3^{\text{alive}} & 0\\ 0 & p_3^{\text{alive}}\end{bmatrix} \\ &\times \begin{bmatrix}\phi_3 & 1-\phi_3\\ 0 & 1\end{bmatrix} \times \begin{bmatrix}p_4^{\text{alive}} & 0\\ 0 & p_4^{\text{alive}}\end{bmatrix} \times \begin{bmatrix}1\\1\end{bmatrix}\end{aligned}$$

which gives the result earlier. The final matrix $\begin{bmatrix}1\\1\end{bmatrix}$ is needed because the two strata cannot be directly observed and an observed tag number could have arisen from either stratum. The initial $\begin{bmatrix}1\\0\end{bmatrix}$ vector is needed because, presumably, all animals were originally released in the alive state. However, the initial matrix could be modified if there were a known acute mortality due to marking effects, or it could be made into a parameter to estimate this acute effect.

The R_1 animals released can be partitioned into mutually exclusive classes based upon their subsequent capture histories. Consequently, assuming that animals are independent of each other, the counts of the number of animals in each capture history class $\{n_\mathbf{h}\}$ can be modelled as a multinomial distribution with the probability of observing the history $\mathbf{h}$ as given above. The likelihood function is then the multinomial probability function

$$L(\{n_\mathbf{h}\}|\{p_i\},\{\phi_i\},\{\theta_i\},\{\nu_i\}) = \binom{R_1}{\{n_\mathbf{h}\}}\prod_\mathbf{h} P(\mathbf{h})^{n_\mathbf{h}}.$$

An additional component could be appended to the likelihood if records are kept of tag numbers reported that are obviously not possible. However, this information is rarely available and this additional component will be ignored.

Because of the complex form of the $P(\mathbf{h})$ terms, there does not appear to be any factorization of the likelihood possible, and it appears that the minimal set of sufficient statistics are the observed capture histories and their corresponding counts.

Inspection of the p_i^{alive} and p_i^{dead} shows that not all parameters are identifiable. In particular, only the products $p_i\theta_i$ (the probability that an animal is captured and its tag read properly) and $p_i(1-\theta_i)\nu_i$ (the probability that an animal is captured, its tag misread, and a valid tag number generated) can be estimated. There is also the usual confounding at the end of the study between ϕ_{K-1} and p_K.

Standard numerical methods can be used to maximize the likelihood function. For example, we used the conjugate gradient optimization method provided in PROC IML of SAS (SAS Institute, Inc. 1995). As in the case with most multistrata models, the likelihood is very flat, and care must be taken not to select a local maximum. As well, in many cases, the misread rate is likely small, and a fully specified model with separate misread rates for each sample time may be too general to be useful. A simpler model would be more useful as a starting point and assumes that θ_i and ν_i are constant over time, i.e., $\theta_i = \theta$ and $\nu_i = \nu$ for all i.

The usual CJS model with no misreads corresponds to the model with $\theta_i = 1$ for all i (with ν_i unspecified). A likelihood ratio test could be constructed to test if the misread rate is 0, but care must be taken in this nonstandard situation because the null hypothesis is on the boundary of the parameter space and is not two-dimensional (Davies 1977; Self and Liang 1987). In this situation, the easiest way to find the significance level of the likelihood ratio test is based upon a parametric bootstrap sample using the estimates from a fit to the standard CJS model (Buckland and Garthwaite 1991; Manly 1997).

Standard errors for the parameter estimates from the misread model can be found using the usual inverse of the information matrix returned by the numerical optimization process. For example, we used a central finite difference method to estimate the information matrix after convergence was obtained. As well, standard errors and confidence intervals for all parameters, but particularly those whose estimates fall on the boundary of the parameter space (e.g., estimates of survival equal to 1), can be found using bootstrap methods on the observed capture histories, as outlined in Buckland and Garthwaite (1991).

Because the likelihood cannot be factored into a smaller set of sufficient statistics, there are no simple goodness-of-fit statistics that "fall out of the likelihood". However, one possible goodness-of-fit test would be to compare the observed and expected counts of tag numbers classified by the number of times the tag number is observed.

Results

Effect of misreads

Case when $\nu_i = 0$

If misreads never generate other valid tag numbers, the likelihood simplifies to that of the standard CJS model except that only the products $p_i\theta_i$ are estimable. It is fairly simple to show that in large sample, $E[\hat{p}_i^{\text{CJS}}|\nu_i = 0] = p_i\theta_i$ and that $E[\hat{\phi}_i^{\text{CJS}}|\nu_i = 0] = \phi_i$, i.e., only estimates of the recapture rates are biased downwards. This is not surprising: misreads

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that never lead to valid tag numbers are indistinguishable from failing to capture the animal.

Case when $\nu_i > 0$

We investigated the likely effects of misreads in these situations by computing the expected CJS summary statistics and then treating the expected values as "data" in the usual estimation formula, as outlined in Lebreton et al. (1992, p. 83).

The probability of observing a tag number corresponding to live and dead animals was derived earlier. Consequently, assuming no losses on capture and no injections at any sample time, the expected number of animals captured and released at time i is found as

$$n_1 = R_1 = N_1$$

$$n_i = m_i = R_i = R_i^{\text{alive}} + R_i^{\text{dead}}$$

$$= N_i p_i^{\text{alive}} + (N_1 - N_i) p_i^{\text{dead}} \quad \text{for } i = 2, \ldots, K.$$

Analogous to similar quantities defined in Lebreton et al. (1992), we compute

$$\lambda_K^{\text{alive}} = 0$$

$$\lambda_i^{\text{alive}} = \phi_i p_{i+1}^{\text{alive}} + \phi_i (1 - p_{i+1}^{\text{alive}}) \lambda_{i+1}^{\text{alive}} + (1 - \phi_i) p_{i+1}^{\text{dead}}$$

$$+ (1 - \phi_i)(1 - p_{i+1}^{\text{dead}}) \lambda_{i+1}^{\text{dead}} \quad \text{for } i = 1, \ldots, K-1$$

$$\lambda_K^{\text{dead}} = 0$$

$$\lambda_i^{\text{dead}} = 1 - (1 - p_{i+1}^{\text{dead}})(1 - \lambda_{i+1}^{\text{dead}}) \quad \text{for } i = 1, \ldots, K-1.$$

Then

$$r_i = R_i^{\text{alive}} \lambda_i^{\text{alive}} + R_i^{\text{dead}} \lambda_i^{\text{dead}}.$$

Finally, using the relationships

$$z_1 = 0$$

$$z_{i+1} = z_i + r_i - m_{i+1} \quad \text{for } i = 1, \ldots, K-1$$

allows us to compute the expected values for all sufficient statistics for the CJS estimates.

There does not appear to be any simple closed-form expressions for the expected values of the ordinary CJS estimators as a function of θ or ν. A simple program to perform the above computations is available from the first author. The results are asymptotic, but simulations using finite samples confirmed the results except for the usual small sample biases introduced into the estimates.

We investigated all possible combinations for $K = 10$ of $\phi = \{0.3, 0.6, 0.9\}$, $p = \{0.1, 0.3, 0.5\}$, $\theta = \{0.80, 0.90, 0.95, 0.99\}$, and $\nu = 0.5$ where all parameters are held constant over time. These represent a range of scenarios likely encountered in practice.

The results for the estimates of survival are shown in Fig. 1. The estimates of survival can be severely positively biased early on in the study, particularly if the misread rate is high. This is caused by the fact that a misread anytime later in the study that generates a tag number corresponding to an already dead animal "implies" that the animal was still alive early in the study. By midstudy, the bias dies out because by then, estimates of survival are based upon animals "known to be alive" from this point onwards, and there are fewer chances that the tag misreads will select animals from this subset. Bias decreases in the early part of the study as the survival rates increase because longer lived animals have a greater chance of legitimately being observed. But this has a price as the bias extends further into the study because the animals are captured more often and each recapture may lead to a misread. The bias appears to be relatively insensitive to values of p because the range of expected values (shown by the small vertical lines) is very small over the values of p examined.

The effects of misreads on the estimates of the capture rate are summarized in Fig. 2. Bias becomes more pronounced as capture rates increase: presumably, more captures lead to greater chances of misreads generating other "valid" tag numbers. The mean of the CJS estimate is close to $p_i\theta_i$, the net probability of seeing an animal and properly reading its tag number, but is usually below this quantity because the misreads generate other valid tag numbers that inflate the apparent population at risk of being captured. Because estimates of abundance are, for the most part, based upon estimates of recapture, this indicates that abundance estimators are positively biased throughout a study. Pradel et al. (1997) noticed that transients tend to cause the Robson (1969) goodness-of-fit test to reject the CJS model. A similar effect is expected to occur in the presence of misreads. In the Robson (1969) goodness-of-fit test, a series of contingency tables for each sample time i ($i = 2, \ldots, K-1$) are constructed of the form:

	Tag numbers subsequently observed after time i	Tag numbers never observed again after time i
Tag numbers first observed at time i		
Tag numbers first observed before time i		

The row corresponding to tag numbers first observed at time i will tend to include misreads that have inadvertently generated a valid tag number from a dead animal, while the row corresponding to tag numbers first observed before time i will tend to include mostly live animals. The probability of subsequent observations of each subset will be different weighted averages of λ_i^{dead} and λ_i^{alive}, and the χ^2 test for homogeneity of proportions will reject the hypothesis of equal subsequent observation rates. Early in the study, the difference in the subsequent observations will be small because many of first-observed animals will, in fact, be valid reads, but the sample sizes will tend to also be large. Later in the study, the first-observed group will be predominately misreads, the difference in the subsequent observation rates will be larger, but sample sizes will be smaller because many animals will not have survived.

The power to detect tag misreads was investigated via computer simulation by generating the expected statistics for the 2×2 contingency tables above used for goodness-of-fit to the CJS model (Lebreton et al. 1992) and treating these as data to obtain the noncentrality parameter as was done in

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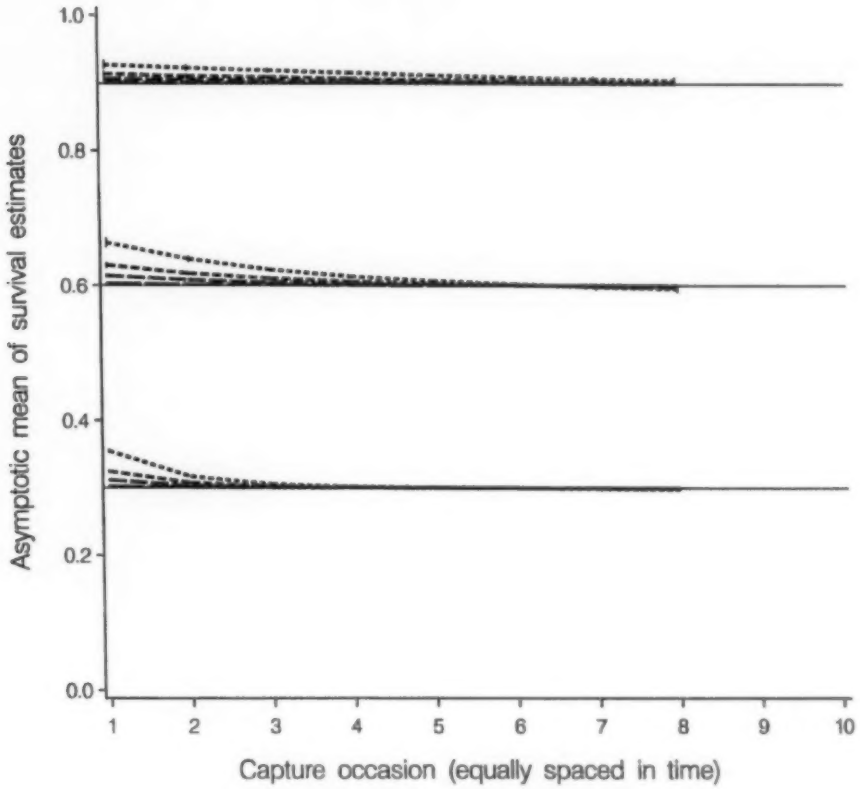
Fig. 1. Approximate expectation of $\hat{\phi}$ in the presence of misreads. Each set of four lines represents (from top to bottom in each set) $\theta = 0.80, 0.90, 0.95$, and 0.99 for $\phi = 0.9, 0.6$, and 0.3, respectively. The vertical bars represent the range of expected values over all combinations of $p = \{0.1, 0.3, 0.5\}$, $\nu = 0.5$, and $K = 10$ with all parameters held constant over all occasions. Note that the vertical bars are extremely small in this graph, indicating that the mean values of $\hat{\phi}$ are very similar over the ranges of p investigated in the simulation.



Burnham et al. (1987, pp. 214–217). We investigated all combinations of $K = \{10, 15\}$, $N_1 = \{250, 500, 1000\}$, $\phi = \{0.3, 0.6, 0.9, 0.95\}$, $p = \{0.1, 0.3, 0.5\}$, $\theta = \{0.80, 0.90, 0.95, 0.99, 1.0\}$, and $\nu = \{0.5, 0.75, 1.0\}$ when all parameters were held constant over time. For $\alpha = 0.10$, the power never exceeded 25% except for combinations where $\phi \geq 0.90$, $p \geq 0.5$, $N_1 \geq 500$, and $\theta \leq 0.90$; even then, the maximal power was only 75% when $K = 10$, but increased substantially and was never below 80% for this subset when K was increased to 15. Power can actually decline if the survival rate is very high; in these cases, most animals survive and misreads only generate tag numbers of animals still alive.

Example applied to seals

Schwarz and Stobo (1997) described a capture–recapture study where cohorts of seal pups on Sable Island were sexed and branded with unique brand numbers. The females return to breed starting at about age 5. During breeding season, multiple surveys of the island are conducted and, at distances of 2–4 m, observers read and record brand numbers of seals spotted. On surveys conducted after inclement weather, the fur of some animals is partially covered with sand or snow; some animals have indistinct brands due to poor application technique, and they may be moving. Multiple observations of the same brand number within a single breeding season are collapsed to a single occurrence of the brand number for that year.

We will demonstrate our methodology using the 1973 female cohort. One additional year of sighting data is now available, and so the summary statistics in this paper differ slightly from those presented in Schwarz and Stobo (1997).

A total of 285 female pups were branded when 1–2 months old with unique brand numbers of the form B*nnn* where *nnn* would represent up to three digits. The values of *nnn* were assigned to pups sequentially with both genders intermingled. Resighting trips took place in 1981, when individuals were 8 years old, and in following years. Some information is available from one earlier year (1978), but the survey work in that year was not systematic. Consequently, that year's information was not used. Also, female seals usually start to recruit to breeding status at age 4, but may not been fully recruited until age 8.

At the end of the field season, the logbooks were returned to the laboratory and transcribed. Cases where obvious illegal brand numbers were reported (e.g., B*xxx* where no seals were branded with *xxx*) were excluded. Unfortunately, the

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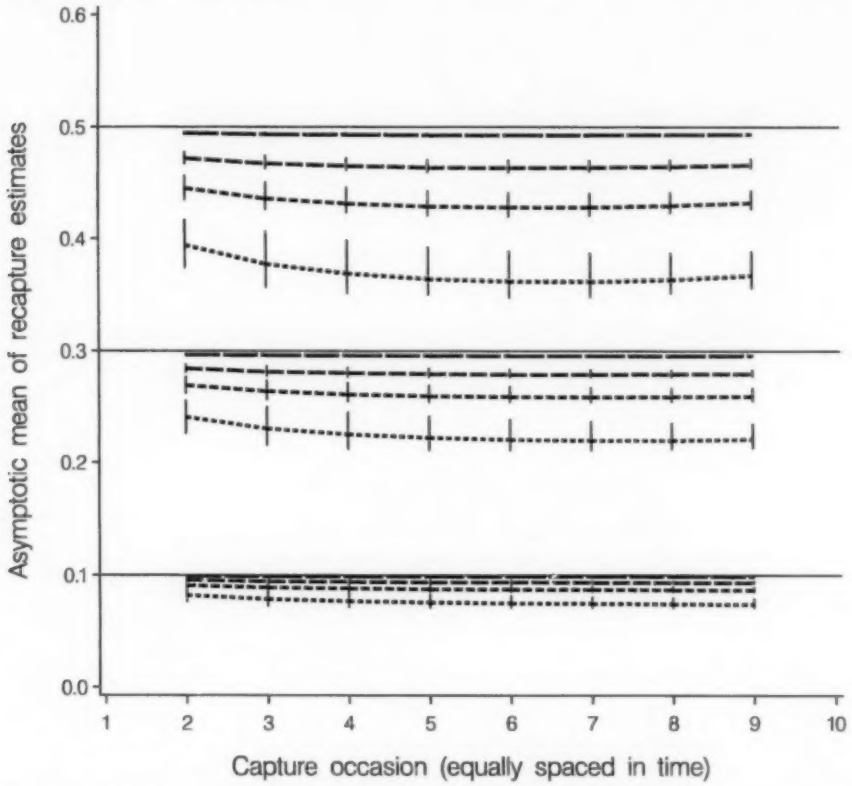
Fig. 2. Approximate expectation of $\hat{p}$ in the presence of misreads. Each set of four lines represents (from top to bottom in each set) $\theta = 0.99$, 0.95, 0.90, and 0.80 for $p = 0.5$, 0.3, and 0.1, respectively. The vertical bars represent the range of expected values over all combinations of $\phi = \{0.3, 0.6, 0.9\}$, $\nu = 0.5$, and $K = 10$.



number of times this occurred is not easily determined; otherwise, this could have provided additional information about the joint probability of making a misread and generating an invalid brand number.

A total of 134 different capture histories were observed. Each capture history consists of a vector of length 15 where $\text{year}_1 = 1973$ (the year of release), $\text{year}_2 = 1981$, $\text{year}_3 = 1982$,..., $\text{year}_{15} = 1994$.

A standard CJS model was fit that corresponds to a model with $\theta = 1$ and $\nu = 0$ (Table 1). A comparison of the observed and expected number of brands by the number of times seen in total during the study (Table 2) showed an obvious lack of fit, particularly with the number of brands reported only once after release. As in our earlier paper (Schwarz and Stobo 1997), the Robson (1969) goodness-of-fit tests strongly rejected this model because there was a large difference between the subsequent sighting probabilities of brands observed for the first time after branding and those previously observed after branding, with the latter much more likely to be resighted in the future. Again, as noted in Schwarz and Stobo (1997), we suspect that the cause is brand misreads.

A model with constant θ and ν over time was fit to the data (Table 1). The likelihood ratio test statistic comparing the standard CJS model (Model 1) with that with θ and ν constant over time (Model 2) is approximately $290 = -2(-1617.7 - (-1472.9))$. The usual large sample χ^2 approximation to the distribution of the test statistic is not applicable in this case because the null hypothesis has the parameters on the boundary of the parameter space and is not two-dimensional (i.e., ν disappears in Model 1). As noted earlier, the significance level was computed from the distribution of the likelihood ratio test statistic formed by a parametric bootstrap using the CJS estimates in Table 1 and is well below 0.001. Table 2 also shows that Model 2 had a dramatic improvement in fit.

The estimated misread rate is approximately 0.10 (SE = 0.015). The probability that a misread generates a valid brand number is estimated to be 1.00 (SE = 0.020 as determined from a bootstrap procedure). This is largely a consequence of the fact that the observers were familiar with the general range of valid brand numbers and of the data cleaning that has taken place in the laboratory, which implies that misreads that generate invalid brand numbers are removed from the data. The bootstrap SE for the estimates in Table 2 were very close to the SE as computed from the inverse of the information matrix (except for those estimates on the bounds of the parameter space). The revised estimates of p_i are much larger than the corresponding estimates under the CJS model, even after multiplying by the estimate of θ (Table 1). The estimates of p_i under the CJS model are severely biased downward, which will severely inflate any estimate of abundance based upon them. Fortunately, Schwarz and

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Table 1. Estimates from three different models applied to the seal data.

	Model 1: $\theta = 1$, $\nu = 0$ (a standard CJS model) (log-likelihood −1617.7)		Model 2: θ and ν constant over time (log-likelihood −1472.9)		Model 3: $\theta = 1$, $\nu = 0$ (a standard CJS model applied to tags seen at least twice)[a]	
	Estimate	SE	Estimate	SE	Estimate	SE
$\hat{p}_{81}$	0.049	0.016	0.061	0.023	0.064	0.021
$\hat{p}_{82}$	0.187	0.030	0.264	0.041	0.250	0.037
$\hat{p}_{83}$	0.374	0.039	0.526	0.050	0.472	0.042
$\hat{p}_{84}$	0.440	0.043	0.643	0.052	0.580	0.042
$\hat{p}_{85}$	0.467	0.043	0.667	0.051	0.573	0.044
$\hat{p}_{86}$	0.569	0.050	0.797	0.048	0.680	0.043
$\hat{p}_{87}$	0.594	0.053	0.782	0.048	0.680	0.044
$\hat{p}_{88}$	0.591	0.054	0.786	0.052	0.669	0.045
$\hat{p}_{89}$	0.677	0.058	0.881	0.048	0.740	0.043
$\hat{p}_{90}$	0.686	0.059	0.866	0.049	0.733	0.044
$\hat{p}_{91}$	0.838	0.065	1.000	0.020[d]	0.869	0.038
$\hat{p}_{92}$	0.779	0.067	0.920	0.048	0.810	0.042
$\hat{p}_{93}$	0.835	0.042	0.938	0.047	0.835	0.041
$\hat{P}_{94}$[b]	1.000	—	1.000	—	1.000	—
$\hat{\theta}$	1.000	—	0.899	0.014	1.000	—
$\hat{\nu}$	0.000	—	1.000	0.020[d]	0.000	—
$\hat{\phi}_{73}$[c]	0.785	0.115	0.637	0.149	0.490	0.030
$\hat{\phi}_{81}$	0.837	0.120	0.744	0.181	1.000	—
$\hat{\phi}_{82}$	1.000	0.015[d]	1.000	0.015[d]	1.000	—
$\hat{\phi}_{83}$	0.995	0.025	0.993	0.024	1.000	—
$\hat{\phi}_{84}$	1.000	0.017[d]	0.980	0.032	0.987	0.028
$\hat{\phi}_{85}$	0.907	0.033	0.928	0.039	0.960	0.026
$\hat{\phi}_{86}$	0.947	0.034	0.991	0.026	0.977	0.020
$\hat{\phi}_{87}$	0.921	0.034	0.961	0.034	0.981	0.021
$\hat{\phi}_{88}$	0.954	0.029	0.948	0.029	0.958	0.024
$\hat{\phi}_{89}$	0.946	0.029	0.988	0.020	0.987	0.017
$\hat{\phi}_{90}$	0.953	0.028	0.974	0.022	0.977	0.020
$\hat{\phi}_{91}$	0.893	0.034	0.954	0.031	0.926	0.029
$\hat{\phi}_{92}$	0.954	0.033	0.965	0.032	0.948	0.032
$\hat{\phi}_{93}$	0.789	0.076	0.930	0.051	0.826	0.044

[a]The log-likelihood was not given for this model because it uses a different set of data (i.e., it discards histories with only one observation after branding).

[b]Only the product $\phi_{93}p_{94}$ can be estimated; $\hat{p}_{94}$ was constrained to the value 1 and hence has no SE reported.

[c]The parameter ϕ_{73} estimates the survival rate from the time of branding in 1973 to the time of the survey performed in 1981.

[d]The SE's for these estimates, which are on the boundary of the parameter space, were determined from bootstrap simulations.

Stobo (1997) showed that a similar inflation also affects the estimated returning population size, and so the effect of misreads cancels when estimating the return rate.

The estimates of survival are less affected, but show that the CJS estimates are likely positively biased at the beginning of the sampling chain and negatively biased from the middle of the study onwards. As noted earlier, this is not surprising. A brand misread late in the study that generates a brand number for a dead animal that died early in the study leads the CJS method to assume that the animal has been alive from the beginning of the study, which tends to inflate earlier estimates. By midstudy, survival estimates are based

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Table 2. Goodness-of-fit test for the three models fit to the seal data.

		Model 1: $\theta = 1$, $\nu = 0$ (a standard CJS model)		Model 2: θ and ν constant over time		Model 3: $\theta = 1$, $\nu = 0$ (applied to tags seen at least twice)[b]	
Times observed[a]	Observed no. of animals	Predicted no. of animals	χ^2	Predicted no. of animals	χ^2	Predicted no. of animals	χ^2
1	100	100.0	0.0	98.5	0.0	146.0	0.0
2	46	13.3	80.8	46.1	0.0	2.9	2.9
3	14	15.6	0.2	14.4	0.0	4.8	17.7
4	6	14.6	5.1	7.2	0.2	5.1	0.2
5	9	13.3	1.4	5.7	1.9	5.3	2.7
6	6	15.1	5.5	5.6	0.0	6.8	0.1
7	8	20.3	7.5	7.4	0.1	10.8	0.7
8	12	26.1	7.7	12.5	0.0	17.5	1.8
9	18	27.6	3.3	20.1	0.2	24.5	1.7
10	17	21.7	1.0	25.5	2.8	26.5	3.4
11	20	12.0	5.4	23.0	0.4	20.5	0.0
12	20	4.3	56.7	13.6	3.0	10.6	8.3
13+[c]	9	1.0	64.0	5.4	2.4	3.8	7.1
Total	285	284.9	238.4	285.0	11.1	285.0	46.6

[a]Includes initial release, i.e., a brand observed once would correspond to a brand number released in 1973, but never again subsequently resighted.

[b]History vectors were modified so that brand numbers observed only twice were reclassified into the observed only once class.

[c]The last few counts were pooled; otherwise, the small value of the predicted number of animals would inflate the cell's χ^2 contribution.

more upon subsequent recoveries of animals known to be alive from that point onwards, and the "nonappearance" of a brand misread looks like a "death", depressing the estimates. However, the bias is not severe because of the long-lived nature of the seal, which allows it to be properly sighted in a future year as well.

In this study, the seals have a high initial mortality after branding, but subsequent survival is high. The surviving animals tend to be seen many times and are usually faithful to their breeding grounds. Yet, we noticed that some brand numbers were observed only once after release. Indeed the goodness-of-fit statistics in Table 2 show a large excess in the number of animals seen twice (at initial branding and only once afterwards). A similar behavior was noted by Pradel et al. (1997) when transients were present, i.e., there could be a subpopulation of seals that only visits Sable Island irregularly. Pradel et al. (1997) suggested that an ad hoc method be used with transients where all brands resighted only once after release are removed prior to an analysis using a standard CJS model. This will completely remove all brands observed only once after branding (corresponding presumably to misreads), but will also remove legitimate histories corresponding to animals suffering an early death. The results of fitting the standard CJS to the modified capture histories are shown in Tables 1 and 2. The estimates of the capture rates seem to have improved early in the study, but show little improvement later in the study. Removal of spurious brand sightings of dead animals late in the study implies that the estimated number of animals alive at the beginning of the study is reduced. This improves estimates of p_i, but later in the study, removal of misreads implies that estimates of p_i tend to estimate the product $p_i\theta$. Estimates of survival are severely affected early in the study because removal of brands observed only once after branding tends to remove histories corresponding to legitimate sightings of animals captured only once before their death, particularly given the low sighting rates and comparably higher mortality rates early in the study. Estimates later in the study are less affected because they are based upon animals typically having a large number of recaptures given the high annual survival and recapture rates late in the study.

A power analysis using the estimates shown in Table 1 with sample sizes similar to those in the study shows that the power to detect misreads in this study is very high, well over 95%. This study was successful in detecting possible misreads because of the relatively lower survival rate after branding until recruitment, which generates a pool of dead animals that misreads can select, and the high subsequent survival and recapture rates, which give a good chance for misreads to occur.

Discussion

This very simple model of tag misreads worked surprisingly well in practice. We suspect that even though misreads do not generate valid numbers from all possible tag numbers, they occur so infrequently that it is not likely that the same misread will take place very often. If the misread rate is higher, this model may not work well, e.g., a tag number 354 may be misread consistently as 854, but a tag number 711 could be misread as 111, 777, or any other combination of 1's and 7's.

One possible alternative explanation for these observed data is the presence of a pool of nonbreeders (transients) who visit Sable Island at extremely irregular intervals. This cannot be ruled out given the observed data, but the current

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model still gives useful estimates of survival of the breeding population and estimates of capture rates that can be used with other cohorts branded in other years to investigate recruitment to breeding status. This model also differs from the transient model of Pradel et al. (1997) in that not only do misreads generate histories that look similar to those from transient animals, but the capture histories of nontransients are also affected.

Tag misreads can also be viewed as a source of heterogeneity in the capture probabilities. Live animals and dead animals are two groups in the populations with different capture probabilities at each sample time. Previous investigations of the effects of heterogeneity in capture probabilities have shown that the estimates of survival are relatively unaffected by modest heterogeneity, while estimates of the capture rates are more sensitive (Pollock et al. 1990). Our results confirm these findings.

Based upon our simulation results and power analyses, misreads could have serious implications in capture–recapture studies where tags are applied to young animals with a high initial mortality until adult age followed by a long period of high survival. In these types of studies, it is often the case that the animal is only physically handled when young, and subsequent recaptures are resightings done at a distance. Under these conditions, estimates of abundance could be severely biased by misreads. When planning studies where future observations have misreads, some care in the actual tag numbers used could reduce the incidence of misreads. For example, the research may avoid using both the digits "1" and "7" in the tag numbers so that they are not confused, or may use tag numbers with a built-in error correcting code. If animals are physically handled, degraded tags should be replaced.

The current models have been fit to data using a general-purpose optimization routine commonly available in many statistical packages or in libraries in other computer languages. The major difficulty in fitting these models using the common mark–recapture software packages such as SURGE, MARK, POPAN, and SURVIV is the complex form of the probability function for each history. A symbolic algebra system could be used to generate the expression that could subsequently be used in SURVIV, but this is not easily done by the casual user. The models could be fit by a general-purose multistrata analysis program (e.g., MS-SURVIV), but these programs assume that the stratum is known when the tag is observed, i.e., the analyst would need to know if the animal is alive or dead when the tag number is observed, and so these programs would also have to be modified.

Acknowledgements

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Periphyton biomass and community composition in rivers of different nutrient status

J. Chételat, F.R. Pick, A. Morin, and P.B. Hamilton

Abstract: Epilithic periphyton was investigated in riffle zones of 13 rivers in southern Ontario and western Quebec to describe how algal biomass and community composition vary with nutrient concentration and water velocity during summer. Algal biomass (milligrams chlorophyll *a* (Chl *a*) per square metre) was strongly correlated with total phosphorus concentration ($r^2 = 0.56$, $p < 0.001$) and conductivity ($r^2 = 0.71$, $p < 0.001$) of the overlying water but unrelated to water velocity over the range of 10–107 cm·s^{-1}. Differences in periphyton Chl *a* were associated with changes in biomass of Chlorophyta ($r^2 = 0.51$, $p = 0.001$) and Bacillariophyta ($r^2 = 0.64$, $p < 0.001$) and were not related to Rhodophyta and Cyanophyta biomass ($p > 0.10$). The relative proportions of taxonomic divisions varied with total standing stock. Percent Chlorophyta biomass increased with periphyton Chl *a* and was the largest fraction at moderately eutrophic sites. Rhodophyta contributed the most biomass at sites with the lowest Chl *a*. *Cladophora*, *Melosira*, and *Audouinella* biomasses were positively correlated with total phosphorus concentration over the range of 6–82 µg·L^{-1} ($r^2 = 0.39$–0.64, $p < 0.005$), and these genera were dominant at sites with the highest nutrient concentrations.

Résumé : On a étudié la végétation épilithique dans des radiers de 13 rivières du sud de l'Ontario et de l'ouest du Québec pour établir comment la biomasse algale et la composition des communautés varient selon la concentration de nutriants et la vitesse du courant durant l'été. La biomasse algale (milligrammes de chlorophylle *a* (Chl *a*) par mètre carré) était fortement corrélée avec la concentration de phosphore total ($r^2 = 0{,}56$, $p < 0{,}001$) et la conductivité ($r^2 = 0{,}71$, $p < 0{,}001$) de l'eau, mais pas avec la vitesse du courant dans la fourchette 10–107 cm·s^{-1}. Les différences dans la Chl *a* de la végétation périlithique étaient associées aux changements dans la biomasse des chlorophytes ($r^2 = 0{,}51$, $p = 0{,}001$) et des bacillariophytes ($r^2 = 0{,}64$, $p < 0{,}001$) et n'étaient pas liées à la biomasse des rhodophytes et des cyanophytes ($p > 0{,}10$). Les proportions relatives des taxons variaient en fonction du stock total. La biomasse de chlorophytes augmentait en pourcentage avec la Chl *a* de la végétation et constituait la fraction la plus importante dans les sites modérément eutrophes. Les rhodophytes constituaient la biomasse la plus importante dans les sites les plus pauvres en Chl *a*. Les biomasses de *Cladophora*, *Melosira* et *Audouinella* étaient positivement corrélées avec la concentration de phosphore total dans la fourchette 6–82 µg·L^{-1} ($r^2 = 0{,}39$–$0{,}64$, $p < 0{,}005$), et ces genres étaient dominants aux sites présentant les plus fortes concentrations de nutriants.

[Traduit par la Rédaction]

Introduction

Epilithic periphyton biomass is highly variable in rivers and can span 6 orders of magnitude (from 0.01 to 10 000 mg chlorophyll *a* (Chl *a*)·m^{-2}; Morin and Cattaneo 1992). In recent years, periphyton proliferations have become more of a concern in urban and rural rivers because they signal problems of eutrophication and can result in the aesthetic degradation of recreational areas. Biggs (1995) suggested that periphyton biomass accrual in rivers is controlled by a combination of resource and disturbance factors. Resource availability (i.e., nutrients, light) determines biomass gain by regulating growth rates, while disturbance factors (i.e., floods, invertebrate grazing) lead to biomass loss through physical removal. There is considerable inconsistency in the literature over the importance of nutrient control, and some studies have found no association between nutrient concentrations and algal standing crop in streams (Jones et al. 1984; Welch et al. 1988; Kjeldsen 1994), while others have indicated strong relationships with phosphorus and nitrogen concentrations (Biggs and Close 1989; Lohman et al. 1992). In the two latter studies, the hydrological regime was also implicated as an important determinant of periphyton biomass. Causal relationships between nutrients and biomass may be complicated by hydrological disturbance events, in which case, nutrient effects should be more apparent during periods of summer low flow.

Most previous studies of periphyton have focused on biomass accrual. Relatively little effort has been placed on determining relationships between trophy and periphyton community structure. And yet, excessive periphyton biomass has been associated not only with nutrient enrichment but also with the growth of particular filamentous taxa such as *Cladophora* (Biggs and Price 1987; Dodds 1991; Welch et

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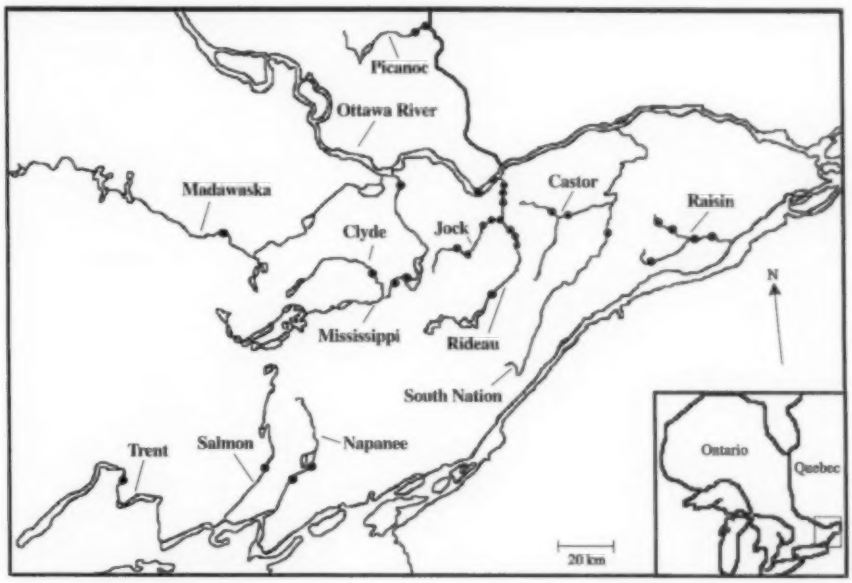
Fig. 1. Location of the 33 sites sampled on 13 rivers in southern Ontario and western Quebec during the summers of 1993, 1995, and 1996.



al. 1992) and *Rhizoclonium* (Biggs and Price 1987). In a study of New Zealand rivers, Biggs (1990) found that conductivity was the variable most strongly related to periphyton communities identified using cluster analysis. Biggs (1990) proposed that conductivity was an indicator of nutrient enrichment in the studied rivers because it was also positively correlated with the area of Tertiary siltstone in the watersheds, a sediment rich in cations and inorganic phosphorus. These observations suggest that nutrient enrichment may affect periphyton standing crop and also cause a shift in community composition towards particular algal taxa that form undesired benthic algal mats.

The purpose of the present study was to investigate the relationship of nutrients to periphyton biomass and community composition during summer low flows. We tested a model incorporating both nutrient concentration and water velocity to determine if water velocity effects could account for more variation in periphyton biomass. Periphyton taxonomy was examined to determine whether community composition changes in relation to trophy and to identify dominant algal taxa.

Materials and methods

Study areas

A total of 33 sites were sampled on 13 temperate lowland rivers in southern Ontario and western Quebec during periods of low flow (Fig. 1). Samples were collected on one occassion at a site between June and August in 1993, 1995, or 1996 (Table 1). The rivers ranged widely in size, with drainage basin areas from 404 km^2 (Raisin River) to 90 900 km^2 (Ottawa River) and summer low flows typically ranging from <1 $m^3 \cdot s^{-1}$ to nearly 700 $m^3 \cdot s^{-1}$ (Water Survey of Canada 1990). Watershed land use also varied among rivers from undisturbed forest to agricultural and urban development.

Epilithic periphyton was sampled in the main channel of shallow riffle zones. Fast-water areas were sufficiently wide (>10 m, except some sites on the Raisin River) and shallow (<0.5 m) to assume that light was not limiting for periphyton growth. Riverbeds were primarily composed of rock substrate.

Field sampling

Rocks were collected randomly from each site by walking across the shallow riffle zone along a transect perpendicular to the shoreline. The number of replicate rocks collected from a site depended on the sampling year (1993, $n = 20$; 1995, $n = 8$; June 1996, $n = 2$; August 1996, $n = 3$). Rocks were roughly fist size and ranged in surface area from 70 to 360 cm^2. Water velocities (centimetres per second) were measured above each rock at a height of 0.4 times the depth (mean current velocity) and just above the substrate (proximal velocity) using a Gurley No. 625 Pygmy current meter. Water conductivity was measured with a Hydrolab in 1995 and YSI model 33 S-C-T probe in 1996. Samples were placed in Ziplock bags, stored in a cooler in the field, kept in a refrigerator in the laboratory, and processed within 24 h of collection.

Periphyton biomass

Periphyton biomass was estimated on each rock from Chl *a* standing stock. First, rocks were scraped with a nylon-bristled nailbrush. The scraped material was washed off the brush and rock with 250–500 mL of filtered river water and then homogenized in a blender. A sample of 5–30 mL of homogenate was filtered through a Whatman HA-195 for Chl *a* analysis. Pigments were extracted with a 10-mL mixture of dimethyl sulfoxide – acetone solvent heated at 65°C for 10 min (Burnison 1980). Spectrophotometer readings were used to calculate Chl *a* with a trichromatic equation (Jeffrey and Humphrey 1975). A 50-mL subsample of periphyton homogenate was also preserved in Lugol's solution for taxonomic identification of the algal community. Rock surface area was estimated by wrapping the rock in aluminum foil and multiplying the mass of the foil by an area/mass conversion factor. Chl *a* (milligrams per square metre) is reported in units of rock surface area

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Table 1. Ranges in mean Chl *a*, TP, and TN concentrations, water conductivity, and current velocity measured at 33 sites on 13 rivers during the summers of 1993, 1995, and 1996.

River	Drainage area (km^2)	Year	No. of sites	Chl *a* ($mg \cdot m^{-2}$)	TP ($\mu g \cdot L^{-1}$)	TN ($\mu g \cdot L^{-1}$)	Conductivity ($\mu S \cdot cm^{-1}$)	Current velocity ($cm \cdot s^{-1}$)
Castor	433	1996	2	311–470	52–82	795–2433	685–723	34–58
Clyde	614	1996	1	14	14	476	264	19
Jock	559	1995	5	38–172	44–130	765–1618	441–495	32–45
Madawaska	8 310	1993	1	27	8	323	na	na
Mississippi	3 780	1996	3	32–59	12–25	383–566	184–225	34–107
Napanee	777	1996	2	40–78	21	560–583	175–191	46–59
Ottawa	90 900	1995	2	17–26	9–10	na	65	10–40
Picanoc	1 290	1996	2	9–12	6–11	200–206	74–101	63–83
Raisin	404	1996	5	42–148	40–76	179–1579	379–547	39–53
Rideau	3 830	1993, 1995	7	85–153	27–42	673–799	362–401	25–41
Salmon	891	1996	1	32	15	429	238	33
South Nation	3 810	1996	1	238	70	2873	560	84
Trent	12 000	1993	1	114	27	577	na	na
Total range and sample size				9–470 (n = 33)	6–130 (n = 33)	179–2873 (n = 30)	65–723 (n = 25)	10–107 (n = 25)

Note: Estimates represent means from one sampling date and do not include temporal variability. TN concentration, conductivity, and current velocity were not measured at all sites (na, not available). Total ranges and sample sizes for each parameter are listed at the bottom of the table. Watershed drainage area for each river was obtained from the Water Survey of Canada (1990).

assuming that periphyton occupied 60% of the stone surface (Biggs and Close 1989).

Nutrient analyses

In 1993 and 1996, three replicate water samples were collected per site at the time of periphyton sampling. In 1995, water chemistry data were obtained from the Regional Municipality of Ottawa–Carleton, Surface Water Quality Branch, who measured nutrient concentrations at corresponding sites within 24–72 h of our periphyton sampling. Chemical analyses were performed by the Regional Municipality of Ottawa–Carleton for all three years. Total phosphorus (TP) was determined by acid digestion to orthophosphorus followed by reaction with ammonium molybdate and ascorbic acid, and total Kjeldahl nitrogen (TKN) was determined by converting organic nitrogen to ammonium sulfate through acid digestion (Regional Municipality of Ottawa–Carleton 1993). Nitrate–nitrite (NO_3–NO_2) was determined by reducing nitrate to nitrite. Nitrite was then diazotized with sulfanilimide and coupled with ethylenediamine dihydrochloride (Regional Municipality of Ottawa–Carleton 1993). Total nitrogen (TN) was calculated as the sum of TKN (unfiltered) and NO_3-NO_2.

Periphyton taxonomy

Seventeen of the 33 sites sampled for periphyton biomass were also examined for algal community composition. We chose a particular subset of samples that were collected over a 7-day period (August 7–14, 1996, 14 sites) in order to avoid the effects of seasonality on periphyton composition. To further broaden the range in trophy, taxonomic samples from three other sites collected between July 22 and 25, 1995, were also included. Three replicate samples were analyzed per site. Each of these samples was a 50-mL subsample from the scraped homogenate used for Chl *a* analysis (see Periphyton biomass above) and was preserved with Lugol's solution.

Identifications were made from aliquots of 0.2–0.5 mL settled in a modified Utermöhl counting chamber and counted using an upright Leitz diaplan or Olympus BH-2 compound microscope with phase and differential interference contrast optics. Benthic algae were identified to genus using Prescott (1973) for non-diatom taxa and Krammer and Lange-Bertalot (1986–1991) for diatoms. Collected algae were assigned to four algal taxonomic divisions: Chlorophyta (green algae), Rhodophyta (red algae), Bacillariophyta (diatoms), and Cyanophyta (cyanobacteria). Small pennate diatoms (i.e., *Achananthes* spp., *Navicula* spp.) were not identified but were counted together in the category "pennate diatoms". Transects were counted at 250 and 500× magnifications. The average number of filament fragments and single-celled algae counted per sample was 368 (n = 51). The number of cells per filament fragment ranged from two to >30. Fragment and cell densities and biomass were calculated for each recorded taxon. Cell dimensions were measured in each sample and cell volumes were estimated by approximation to geometric shapes of known volume. Algal biomass was measured by converting calculated cell volumes to biomass assuming a specific density of 1 $g \cdot cm^{-3}$. Algal biomass (micrograms per square centimetre) was calculated in units of rock surface area assuming that periphyton occupied 60% of the stone surface and was averaged over three replicates to determine mean biomass levels for each site.

Data analysis

Estimates of Chl *a*, nutrient concentrations, conductivity, water velocity, and taxonomic biomass represent site means from one sampling date and do not include temporal variability. TN concentration, conductivity, and water velocity were not measured at all sites.

Relationships between trophy and periphyton biomass and community composition were examined by linear regression analysis. Periphyton Chl *a* (milligrams per square metre) was regressed against TN (micrograms per litre), TP (micrograms per litre), and conductivity (microsiemens per centimetre). Each regression was performed separately due to high multicollinearity of the predictor variables. Division and genus biomass (micrograms per square centimetre) were regressed against Chl *a* (milligrams per square metre) and TP (micrograms per litre). Mean current velocity and proximal velocity (centimetres per second) were tested as predictors of the residual variation in each regression model. Trends of percent division biomass in relation to periphyton standing crop

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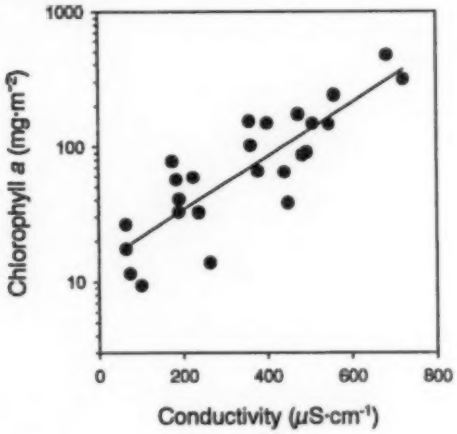
Table 2. Summary of regression models relating periphyton Chl *a* ($mg \cdot m^{-2}$) to water conductivity ($\mu S \cdot cm^{-1}$) and TP and TN concentration ($\mu g \cdot L^{-1}$).

Equation	r^2	F	RMS	p	n
log Chl *a* = 0.002 conductivity + 1.134	0.71	59.5	0.058	<0.001	25
log Chl *a* = 0.905 log TP + 0.490	0.56	41.6	0.071	<0.001	33
log Chl *a* = 0.984 log TN – 0.935	0.50	30.2	0.079	<0.001	30

Note: All variables required log transformation except conductivity. The coefficient of determination (r^2), F value, residual mean square (RMS), p value, and number of observations (n) are presented for each model.

Fig. 2. Regressions of periphyton Chl *a* as a function of water conductivity ($r^2 = 0.71$, $p < 0.001$, $n = 25$) and TP concentration ($r^2 = 0.56$, $p < 0.001$, $n = 33$). All variables are log transformed except conductivity.



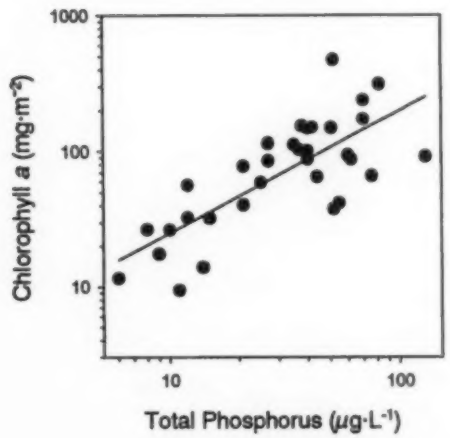
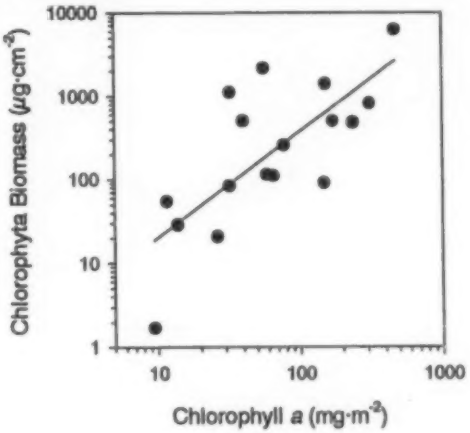
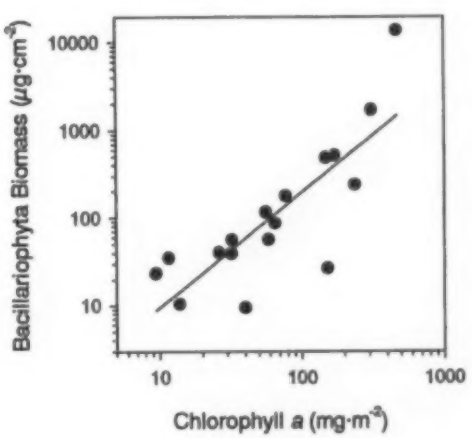


Fig. 3. Regressions of periphyton Chl *a* in relation to Chlorophyta biomass ($r^2 = 0.51$, $p = 0.001$, $n = 17$) and Bacillariophyta biomass ($r^2 = 0.64$, $p < 0.001$, $n = 17$). Variables are log transformed.





were nonlinear and were examined with a model-free, locally weighted sequential smoothing technique (LOWESS).

Statistical analyses were performed using Systat (Wilkinson 1996). For multiple regression analyses, a second independent variable was included if it improved the fit of the model. Significance of a term was tested using coefficients of determination from the higher and reduced models to calculate an F statistic (Sokal and Rohlf 1995). Variables were log transformed or $\log(Y + 1)$ transformed (if the biomass of a genus was zero at a site) to meet the assumptions of the parametric test.

Results

Periphyton biomass

Periphyton Chl *a* was positively related to water conductivity and ambient nutrient concentrations. Chl *a* ranged from 9 to 470 $mg \cdot m^{-2}$ among sites, while TP and TN ranged from 6 to 130 and from 179 to 2873 $\mu g \cdot L^{-1}$, respectively (Table 1). The study rivers drained watersheds of either granitic Canadian Shield or St. Lawrence Lowland sedimentary bed-

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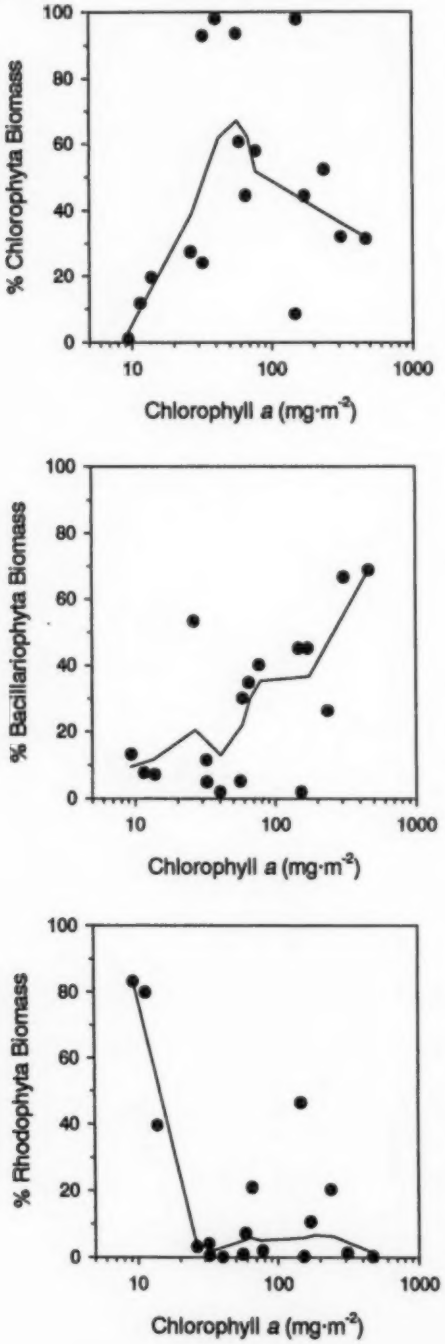
Fig. 4. Relationships between percent contribution of taxonomic groups (Chlorophyta, Bacillariophyta, Rhodophyta) and periphyton Chl *a*. Data are fitted with a locally weighted smoothing technique (LOWESS). Periphyton Chl *a* is log transformed.



rock, and water conductivities reflected these differences in underlying geology with values ranging from 65 to 723 $\mu S \cdot cm^{-1}$. Chl *a* was most strongly related to conductivity ($r^2 = 0.71$), but ambient TP and TN concentrations also explained 56 and 50% of the variation, respectively (Fig. 2; Table 2). TN and TP were positively correlated with water conductivity ($r^2 > 0.70$, $p < 0.001$), suggesting strong relationships between concentrations of nutrients and drainage basin characteristics. Furthermore, TP, TN, and conductivity were negatively correlated with the drainage basin area (square kilometres) of study sites (TP: $r^2 = 0.26$, $p = 0.002$; TN: $r^2 = 0.13$, $p = 0.034$; conductivity: $r^2 = 0.27$, $p = 0.006$), indicating that nutrients tended to be slightly higher in smaller rivers. The collinearity between nutrients, conductivity, and drainage area precluded these factors from being related to Chl *a* in a multiple regression model.

Chl *a* standing stock, once corrected for nutrient concentration or conductivity, was not related to water velocity. Multiple regression analysis was performed to determine if mean current velocity and proximal velocity could explain any of the residual variation in Chl *a* when TP, TN, and conductivity were used as predictor variables. Sample sizes were lower in the multiple regressions (TP, $n = 25$; TN, $n = 23$; conductivity, $n = 25$) because water velocity data were not available for all sites. Neither velocity parameter accounted for more than 2% of Chl *a* variation in the three models ($F \leq 0.9$, $p > 0.05$) despite the wide range in mean current velocities (10–107 $cm \cdot s^{-1}$, Table 1).

Periphyton community composition

Differences in periphyton standing stock were related to changes in Chlorophyta and Bacillariophyta biomass. Chlorophyta and Bacillariophyta biomasses ranged 4 orders of magnitude among sites from 2 to 6226 and from 9 to 13 647 $\mu g \cdot cm^{-2}$, respectively. Rhodophyta and Cyanophyta biomasses tended to be lower but also ranged 4 orders from 0.2 to 495 and from 0.5 to 209 $\mu g \cdot cm^{-2}$, respectively. Chlorophyta and Bacillariophyta biomasses were positively correlated with periphyton Chl *a* (Fig. 3), whereas Rhodophyta and Cyanophyta biomasses were not ($p > 0.10$). Biomass of each taxonomic division was not related to mean current velocity or proximal velocity ($F \leq 1.2$, $p > 0.05$).

The relative proportions of taxonomic divisions varied with total standing stock. Overall, Chlorophyta accounted for the highest portion of biomass, averaging 47% among sites. Bacillariophyta, Rhodophyta, and Cyanophyta represented smaller fractions of total biomass, averaging 27, 19, and 7%, respectively. Percent Chlorophyta biomass increased with periphyton Chl *a* and was the largest fraction at moderately eutrophic sites (Fig. 4). At the highest standing crops, the percent biomass of Chlorophyta decreased with an associated increase in the proportion of Bacillariophyta. Rhodophyta contributed the most biomass at sites with the lowest Chl *a* (Fig. 4). Cyanophyta represented <3% of total biomass at 80% of the sites.

Particular algal genera were dominant at nutrient-enriched sites. Genera were ranked by highest percent contributors to site total biomass and were considered dominant if they were among the top ranking taxa that cumulatively accounted for 70% of total biomass. Despite the wide variation in dominant algal genera among rivers, patterns were observed

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Table 3. Dominant genera of river periphyton communities.

River and site No.	TP ($\mu g \cdot L^{-1}$)	TN ($\mu g \cdot L^{-1}$)	Conductivity ($\mu S \cdot cm^{-1}$)	Dominant genera (%)
Picanoc 1	6	200	74	*Boldia* (76)
Ottawa 3	10	—	65	*Gomphonema* (45), *Coleochaete* (25)
Picanoc 2	11	206	101	*Boldia* (70)
Mississippi 2	12	383	183	*Spirogyra* (90)
Mississippi 3	12	386	190	*Oedogonium* (73)
Clyde 1	14	476	264	*Audouinella* (40), *Lyngbya* (31)
Salmon 1	15	429	238	*Tolypothrix* (60), *Oedogonium* (23)
Napanee 2	21	583	175	*Rhizoclonium* (51), *Cocconeis* (30)
Napanee 1	21	560	191	*Cladophora* (98)
Mississippi 1	25	566	225	*Cladophora* (41), *Coleochaete* (20), pennate diatoms (14)
Rideau 3	38	688	358	*Cladophora* (68), *Hydrodictyon* (17)
Raisin 7	51	1170	509	*Audouinella* (46), *Melosira* (32)
Castor 2	52	795	685	*Melosira* (61), *Cladophora* (30)
Jock 2	70	942	475	*Cladophora* (44), *Melosira* (20), *Audouinella* (11), *Cymbella* (11)
South Nation 1	70	2873	560	*Cladophora* (48), *Audouinella* (20), *Melosira* (10)
Raisin 2	76	1579	379	*Cladophora* (31), *Audouinella* (21), pennate diatoms (14), *Oedogonium* (13)
Castor 1	82	2433	723	*Melosira* (57), *Cladophora* (30)

Note: Taxonomic samples were collected in late July or mid-August, and three replicate samples were analyzed per site. Genera are ranked by highest percent contributors to site total biomass and were considered dominant if they were among the top ranking taxa that cumulatively accounted for 70% of total biomass. River sites are ranked by TP concentration.

along a TP gradient (Table 3). There was a high diversity of periphyton communities among sites with TP concentrations <20 $\mu g \cdot L^{-1}$. In contrast, *Cladophora*, *Audouinella*, and (or) *Melosira* were dominant taxa at sites with TP roughly >20 $\mu g \cdot L^{-1}$ (Table 3).

Cladophora represented a large fraction of Chlorophyta biomass at nutrient-enriched sites. Although 16 genera of Chlorophyta were identified, including eight filamentous taxa, *Cladophora* accounted for >65% of green algal biomass at sites with TP concentrations >20 $\mu g \cdot L^{-1}$ (Fig. 5). Other green macroalgae, primarily *Spirogyra*, *Oedogonium*, and *Coleochaete*, represented a large fraction of Chlorophyta biomass at nutrient-poor sites (Fig. 5). *Cladophora* biomass was strongly correlated with ambient TP concentration (Fig. 6) and was unrelated to mean current velocity or proximal velocity ($F \leq 0.2$, $p > 0.05$). Conductivity also had a positive effect on *Cladophora* biomass after controlling for the effect of TP concentration (Fig. 6). *Cladophora* was recorded at all sites except for those with the lowest TP concentrations ($\leq$ 11 $\mu g \cdot L^{-1}$) and conductivities ($\leq$ 101 $\mu S \cdot cm^{-1}$) on the Ottawa and Picanoc rivers.

The diatom *Melosira* also responded positively to nutrient enrichment. *Melosira* biomass increased with TP concentration ($r^2 = 0.64$, $p < 0.001$) and was a dominant contributor to both Bacillariophyta biomass (Fig. 5) and total biomass (Table 3) at eutrophic sites. *Gomphonema* represented a significant portion of diatom biomass at some low-TP sites, and there was a shift in dominance from *Cocconeis* to *Melosira* between intermediate to high TP concentrations (Fig. 5). These trends describe only major changes in Bacillariophyta composition, and more than 16 diatom genera were identified, some of which were important taxa at a few sites (i.e., *Achananthes*, *Cymbella*, *Navicula*, *Amphora*). Nutrients may have indirectly affected diatom composition by stimulating the growth of filamentous biomass and thereby increasing the surface area available for colonization by epiphytic taxa. This is suggested by the positive relationship between TP concentration and biomass of the epiphytes *Cocconeis* ($r^2 = 0.32$, $p = 0.010$) and *Rhoicosphenia* ($r^2 = 0.56$, $p < 0.001$).

Audouinella, a red filamentous alga, was a dominant taxon in a few nutrient-enriched rivers (Table 3). Only three Rhodophyta genera were identified, one (*Audouinella*) of which represented 100% of red algal biomass at the majority of sites. The two other genera, *Batrachospermum* and *Boldia*, were only found in the low-nutrient and low-conductivity Picanoc River. *Audouinella* was present at all sites examined for taxonomy, and its biomass was positively correlated with TP concentration ($r^2 = 0.39$, $p = 0.004$) and not related to mean current velocity or proximal velocity ($F \leq 0.8$, $p > 0.05$).

Discussion

Periphyton biomass was strongly related to ambient TP concentration. Biggs and Close (1989) and Lohman et al. (1992) also found strong correlations in which TP explained 47–60% of the variation in periphyton Chl *a* (compared with 56% in this study). For the purpose of comparison with our model, their TP and Chl *a* data were log transformed and regressed (Table 4). The slope of our model was similar to that of Biggs and Close (1989) who sampled New Zealand rivers of comparable size with drainage areas from <164 to 2626 km^2 (Table 4). However, the slope of our model was three or four times greater than those of Lohman et al. (1992) who sampled streams mostly smaller than fourth order (Table 4). The difference in slopes may reflect a reduced effect of nutrients on periphyton biomass in stream versus river systems (Lamberti and Steinman 1997). Other stream studies have found no association between nutrients and periphyton Chl *a* (Jones et al. 1984; Welch et al. 1988). Flood events can strongly regulate periphyton biomass in streams (Lohman et al. 1992), but larger rivers tend to have more stable flow

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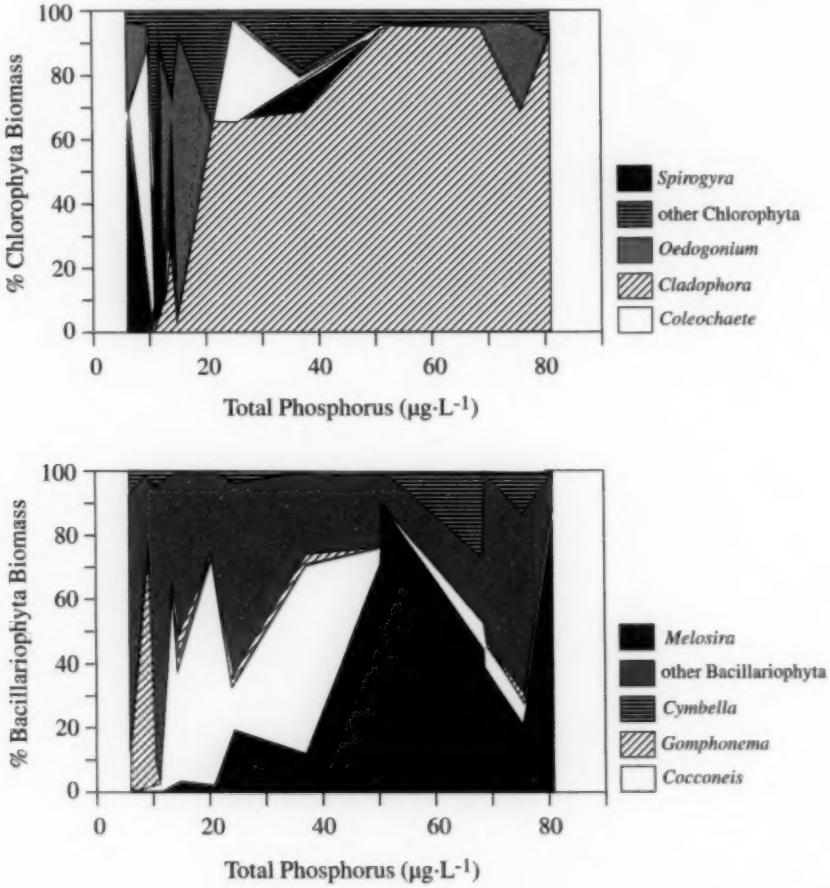
Fig. 5. Area plots of percent contribution of dominant genera to Chlorophyta biomass or Bacillariophyta biomass in relation to TP concentration.



regimes (Poff and Ward 1989; Jowett and Duncan 1990). Thus, riffle zones in larger rivers may represent environments where hydraulic disturbance is less important in periphyton dynamics simply because flood events are less frequent. In the study by Biggs and Close (1989), three lowland rivers exhibited particularly low hydrological disturbance regimes, and they positively influenced the slope of the model. However, the importance of stream size is speculative, and differences in the log TP – log Chl *a* models may simply reflect regional differences in the ecosystem processes that regulate biomass accrual.

Current velocity and proximal velocity were not related to periphyton biomass. There have been conflicting results reported in the literature with respect to water velocity effects (Stevenson 1996). Current can stimulate biomass accrual by increasing nutrient transport to cells and can also reduce biomass through drag (Stevenson 1996). The particular velocity effect depends on the nutrient regime (Horner and Welch 1981) and the morphology of the periphyton community (Biggs et al. 1998). Biggs et al. (1998) found that within-site patchiness in periphyton biomass was strongly related to current velocity but the effect differed for various community growth forms (mucilaginous diatoms, stalked/short filamentous diatoms, long green filamentous algae). Because this study's survey data set was composed of sites with varying community morphologies and nutrient regimes, it is perhaps not surprising that no relationship between water velocity and biomass was observed. Water velocity should better predict periphyton biomass at smaller scales of observation (i.e., within-site patchiness) where more homogeneous nutrient regimes and community types are found.

Composition of the periphyton communities changed in relation to trophy. Higher periphyton standing stocks were primarily associated with increases in green algae and diatom biomass. Filamentous green algae represented the largest fraction of community biomass at moderately eutrophic sites. Proliferations of benthic filamentous Chlorophyta have been commonly associated with nutrient enrichment in both lotic (Perrin et al. 1987; Biggs 1990) and lentic environments (Cattaneo 1987; Jacoby et al. 1991). There was a shift in the dominance among green algal taxa from *Spirogyra*, *Oedogonium*, and *Coleochaete* at low TP concentrations to *Cladophora* above 20 µg TP·L^{-1}. Changes in the diatom community were also observed with the appearance of *Melo-*

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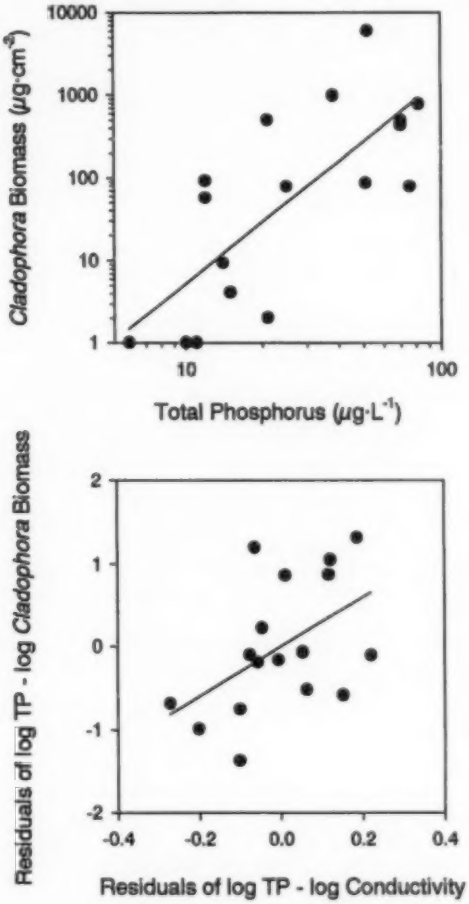
Fig. 6. Regressions of *Cladophora* biomass in relation to TP concentration (log *Cladophora* biomass = 2.500 log TP – 1.820; $r^2 = 0.53$, $p = 0.001$, $n = 17$) and water conductivity ($r^2 = 0.20$, $p = 0.041$, $n = 17$) after controlling for the effect of TP. Conductivity and TP are log transformed and *Cladophora* biomass is log(Y + 1) transformed.



sira at nutrient-enriched sites. *Melosira* and *Cladophora* were similarly reported as dominant taxa for higher biomass sites in New Zealand rivers (Biggs and Price 1987).

At the highest standing crops, the relative contribution of Chlorophyta decreased with an associated increase in Bacillariophyta. This proportional decrease in Chlorophyta biomass does not necessarily indicate a reduction in the competitive success of green algae. Rather, the percent increase in diatom biomass may reflect the ability of these taxa to successfully colonize microhabitat created by thick filamentous mats (i.e., increased surface area for colonization). Diatoms are highly successful colonizers and can contribute 30–60% to total biomass of *Cladophora* mats in nutrient-rich waters (Stevenson and Stoermer 1982). However, at a few eutrophic sites, the red algal filament *Audouinella* was a dominant taxon, suggesting that this genus can successfully compete for substrate space in the presence of filamentous greens, primarily *Cladophora*. The species of *Audouinella* observed in the study rivers, *Audouinella hermannii*, is widespread throughout North America and is most common in temperate regions (Sheath and Cole 1992). Despite its prevalence, little is known of the effect of nutrients on its distribution, and these findings indicate that this species is able to thrive in nutrient-enriched waters.

Nutrient kinetic theory provides a framework for our field observations that periphyton biomass and community composition are related to nutrients. During summer, when periphyton is exposed to high water temperatures (≥ 20°C) and abundant light in shallow unshaded riffle zones, nutrient availability is likely the primary determinant for benthic algal growth rates. Periphyton biomass measured in this study was not related to summer water temperatures. Nutrients also regulate peak standing crops because biomass accrual reduces nutrient diffusion within benthic mats and causes a shift from cellular to whole-mat growth kinetics (Bothwell 1989). Molecular diffusion of nutrients across the boundary layer of periphyton is a key process affecting the metabolism of the community (Riber and Wetzel 1987), and higher ambient nutrient concentrations continue to stimulate biomass accrual because larger nutrient gradients increase diffusion into thick deficient mats. Bothwell (1989) demonstrated that peak biomass of periphytic diatom communities increased over 100 mg Chl $a \cdot m^{-2}$ with additions of phosphorus concentrations greater than those required to achieve maximum growth rates in thin diatom films. Field observations by Lohman et al. (1992) also indicated that following a catastrophic flood, both the rate of biomass accrual and the peak recovery standing crops of periphyton were higher at more nutrient-enriched sites.

The distribution and abundance of benthic algae may also be in part related to taxa-specific nutrient kinetics. Periphytic algae have wide-ranging nutrient requirements for maximum growth rates from 0.5–1 µg $P \cdot L^{-1}$ for diatoms (Bothwell 1989) to 25–40 µg $P \cdot L^{-1}$ for filamentous greens such as *Stigeoclonium* or *Cladophora* (Rosemarin 1983) or even 60 µg $TP \cdot L^{-1}$ for *Cladophora* (Wong and Clark 1976). Borchardt et al. (1994) examined phosphorus uptake kinetics in *Spirogyra fluviatilis*, and they concluded that this species would best thrive under low steady supplies of phosphorus. In contrast, *Cladophora* has relatively high phosphorus requirements for optimal growth (Wong and Clark 1976; Rosemarin 1983). Our observation that *Spirogyra* was an important green algal filament at low TP concentrations whereas *Cladophora* dominated at higher TP coincides with predictions based on nutrient kinetic experiments.

Ecological information on *Cladophora* growth is of particular interest because nuisance proliferations of this filamentous genus are widespread (Wong and Clark 1976; Biggs and Price 1987; Dodds 1991). In the present study, *Cladophora* biomass increased with TP concentration, and a similar relationship was also observed with total inorganic phosphate in British rivers (Pitcairn and Hawkes 1973). Wong and Clark (1976) observed a positive correlation between ambient phosphorus concentration in the water and phosphorus content of *Cladophora* tissue in southern Ontario rivers. No correlation was found with tissue nitrogen, suggesting that *Cladophora* growth was phosphorus limited. Water hardness may be another chemical determinant of *Cladophora* biomass in rivers. *Cladophora* has long been

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Table 4. Regression of periphyton Chl *a* ($mg \cdot m^{-2}$) as a function of TP concentration ($\mu g \cdot L^{-1}$) from the present study in comparison with other models obtained from the literature.

Coefficients						
Intercept (±SE)	log TP (±SE)	r^2	RMS	*p*	*n*	Source
0.490±0.213	0.905±0.140	0.56	0.071	<0.001	33	Present study
0.338±0.310	0.722±0.246	0.49	0.089	0.022	9	Biggs and Close 1989
1.207±0.115	0.247±0.056	0.46	0.038	<0.001	22	(*i*) Lohman et al. 1992
1.383±0.095	0.228±0.047	0.52	0.025	<0.001	22	(*ii*) Lohman et al. 1992

Note: Data sources: Biggs and Close (1989) (data are geometric annual means from nine New Zealand rivers) and Lohman et al. (1992) (data are annual means from 22 sites on 12 Northern Ozark streams for (*i*) 1985 and (*ii*) 1986). Data are log transformed. The coefficient of determination (r^2), residual mean square (RMS), *p* value, and number of observations (*n*) are presented for each model.

suspected to favor hard waters for growth (Whitton 1970), and the positive relationship between conductivity and *Cladophora* biomass after controlling for the effect of TP lends support to the idea that Ca^{2+} concentration is important (Sikes 1978). Sikes (1978) reported a high affinity for calcium by *Cladophora glomerata* which was associated with the thickening of its cell walls.

Neither temporal variability in nutrients and water velocity or invertebrate grazing was explored in this study and may account for unexplained variation. Water samples collected at the time of periphyton sampling may not have been an accurate reflection of nutrient loading due to temporal variability in water chemistry, and estimates of biomass on one sampling date represented growth accumulation over time. Furthermore, water velocities measured at the time of sampling were only coarse estimates of the average hydraulic conditions encountered by periphyton and may have been inadequate to estimate water velocity effects. Invertebrate grazing is believed to affect periphyton and has been demonstrated to remove large amounts of periphyton Chl *a* and alter algal assemblages in experimental studies (Feminella and Hawkins 1995).

In summary, biomass and taxonomic composition of river periphyton from riffle zones were strongly related to ambient nutrient concentrations but unrelated to water velocity. Nutrient-rich sites were associated with high periphyton standing crop and were dominated by particular filamentous taxa. TP concentration was strongly correlated with periphyton Chl *a* and *Cladophora* biomass during summer low flows, but these relationships may not hold during other seasons and periods of high flow.

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Relationship between chinook salmon (*Oncorhynchus tshawytscha*) redd densities and PHABSIM-predicted habitat in the Merced and Lower American rivers, California

Sean P. Gallagher and Mark F. Gard

Abstract: An index of chinook salmon (*Oncorhynchus tshawytscha*) spawning habitat predicted using the physical habitat simulation system (PHABSIM) component of the instream flow incremental methodology was compared with redd densities and locations for sites in the Merced River, California, during 1996 and with redd numbers in sites in the Merced and Lower American rivers, California, from 1989 through 1996. Predicted weighted useable area (WUA) was significantly correlated with chinook salmon spawning density and location at five of seven sites in the Merced River. At the microhabitat level, in the Merced River during 1996, there was a significant relationship between chinook salmon redd location and predicted WUA. Cells with more WUA in the Merced River tended to have more redds. At the mesohabitat level, there was a significant relationship between redd density and predicted WUA in both rivers. Transect areas in the Merced River with higher predicted WUA had more redds. Sites with higher numbers of redds had more predicted WUA. Significant correlations between predicted WUA and spawning locations increase confidence in the use of PHABSIM modeling results for fisheries management in the Merced and Lower American rivers as well as in other rivers.

Résumé : On a comparé un indice des frayères du quinnat (*Oncorhynchus tshawytscha*), établi au moyen du système de simulation de l'habitat physique (PHABSIM) de la méthode incrémentielle de l'écoulement en rivière, aux densités et aux emplacements des nids dans des sites de la rivière Merced (Californie) en 1996 et au nombre de nids dans des sites des rivières Merced et Lower American (Californie) de 1989 à 1996. L'aire utilisable pondéré prévue était significativement corrélée avec la densité et la localisation des quinnats en fraye à cinq des sept sites de la Merced. À l'échelle du microhabitat, dans la Merced en 1996, il y avait une relation significative entre l'emplacement des nids de quinnat et l'aire utilisable pondérée prévue. Les cellules de la Merced où l'aire utilisable pondérée était plus grande tendaient à renfermer plus de nids. À l'échelle du mésohabitat, il y avait une relation significative entre la densité des nids et l'aire utilisable pondérée prévue dans les deux rivières. Les transects de la Merced où l'aire utilisable pondérée prévue était plus grande renfermaient plus de nids. Les sites renfermant le plus de nids comportaient une aire utilisable pondérée prévue plus importante. Les corrélations significatives entre l'aire utilisable pondérée prévue et les emplacements de la fraye accroissent la confiance qu'on peut avoir dans les résultats de la modélisation fondée sur le PHABSIM pour la gestion des pêches dans la Merced et la Lower American ainsi que dans d'autres rivières.

[Traduit par la Rédaction]

Introduction

Relationships between fish population levels and physical habitat simulation system (PHABSIM) (Milhous et al. 1989) habitat predictions have had mixed results (Conder and Annear 1987; Shirvell 1989). While PHABSIM is used extensively for predicting potential habitat with changes in stream flow, validation of relationships between model predictions and fish population levels has received little attention (Reiser et al. 1989). By applying life stage specific habitat suitability criteria for depth, velocity, substrate, and cover, PHABSIM predicts depth and velocity across a channel and combines them with substrate or cover into a habitat index known as weighted useable area (WUA) (Bovee 1982; Milhous et al. 1989). The WUA output is generally simulated for river reaches over a range of stream flows. The PHABSIM operates under the assumption that if physical habitat is a limiting factor, the quality and quantity of available habitat (i.e., WUA) for a limiting life stage during a limiting flow event are directly related to fish population levels. This implies that fish will use higher quality habitat (identified by PHABSIM) more often than habitat of lower quality and that the amount of habitat should translate into fish production (Bovee 1982). Users of PHABSIM assume that WUA predicted by PHABSIM is a consistent measure of quality and quantity of habitat. The validity of this assumption has long been debated (Orth and Maughan 1982; Mathur et al. 1985; Conder and Annear 1987; Orth 1987; Scott and Shirvell

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Table 1. Merced River study site locations and number of transects at each site.

Site	River km	No. of transects
1	83.7	5
2	74.0	5
3	73.5	3
4	73.2	2
5	72.1	6
6	70.5	3
7	69.8	4

1987; Castleberry et al. 1996). Conder and Annear (1987) suggested that the relationship between WUA and fish population levels is unique to each stream and that PHABSIM predictions should not be used before relationships are shown.

We examined the relationship between chinook salmon (*Oncorhynchus tshawytscha*) spawning and WUA predictions from PHABSIM at the microhabitat and mesohabitat levels in the Merced River, California, and at the mesohabitat level in the Lower American River, California. We compared chinook redd density and locations with predicted WUA cell by cell, by transect, and at the mesohabitat level using an in-river approach. The purpose of this study was to test the consistency of WUA as an index of habitat at different spatial and temporal scales when transects were placed in sites known to be heavily used for spawning.

Study sites

The study was part of investigations conducted by the U.S. Fish and Wildlife Service and the California Department of Fish and Game to identify instream flow requirements for anadromous fish in streams within the Central Valley of California, pursuant to the Central Valley Project Improvement Act. The rivers selected for study were chosen because they are major regulated Central Valley streams for which additional investigations are needed to identify instream flow requirements.

The Merced River, located in the San Joaquin River basin, and the Lower American River, located in the Sacramento River basin, drain 2693 and 5376 km^2, respectively, along the western flank of the Sierra Nevada Mountains in California (Fig. 1). The Merced and Lower American rivers have a mean annual flow of 18.7 and 106 m^3/s, respectively. Both rivers have hatcheries that contribute to fall-run chinook salmon production and are located at the upstream limit to anadromous fish migration. The Merced River portion of this study was conducted in a 16-km reach directly below Crocker–Huffman Dam, while the American River portion of the study was conducted in a 9-km reach 1.5 km below Nimbus Dam (Fig. 1). The two study reaches were chosen because they were the portions of the Merced and American rivers with the highest use by spawning fall-run chinook salmon during the past decade (CDFG 1994, 1996; USFWS 1996, 1997). Seven sites were selected in the Merced River and 10 sites in the American River for measuring chinook salmon redd microhabitat characteristics and modeling available habitat.

Materials and methods

Field measurements

To model chinook spawning WUA, we collected physical and hydraulic data along transects for input into the hydraulic and habitat simulation models within PHABSIM using procedures outlined in Trihey and Wegner (1981). We placed transects in the Merced and Lower American River study sites across the optimal spawning areas based on substrate size and past redd distributions. Table 1 lists the river location and number of transects at each site on the Merced River. Twenty transects, two at each study site, were placed on the Lower American River. Lateral cell boundaries were established across each transect systematically or where differences in bed elevations, water velocity, or substrate composition occurred. Cell boundaries were established halfway between adjacent measurement points, so that the center of each cell was at a measurement point. The average number of cells, cell area, cell width, and distance between transects for the Merced and American rivers are shown in Table 2. Dominant substrate was visually assessed using a modified Brusven index (Platts et al. 1983). We collected cell depths, velocities, and substrate data at flows of 11.95–13.36 m^3/s for the Merced River during October 1996 and 70.8–84.9 m^3/s for the American River during August 1996. We measured water surface elevations and discharges at three or four flows for each site. These flows ranged from 28.3 to 113.3 m^3/s for the American River during August–October 1995 and from 2.32 to 32.7 m^3/s for the Merced River during August–October 1996 (USFWS 1996, 1997).

To develop chinook salmon spawning habitat suitability criteria, we collected depth, velocity, and substrate data on 186 fall-run chinook salmon redds in the Merced River between 12 and 14 November 1996 at a flow of 7.79 m^3/s and on 218 fall-run chinook salmon redds on the Lower American River on 6 and 7 November 1996 at a flow of 78.6 m^3/s (Table 3). Flows were stable in both rivers from the beginning of the spawning period through the dates of data collection. All newly constructed redds (redds without periphyton) at each site were measured. Depth and water column velocity data were collected 0.5 m upstream of the redd pot, where hydraulic conditions were assumed to be similar to those at the redd location prior to construction. Dominant substrate was visually assessed in the tail spill using a modified Brusven index (Platts et al. 1983). We used horizontal surveying to determine the locations of 151 redds relative to our transects at the seven studies sites in the Merced River.

Habitat modeling

Average water column velocities, water surface elevations, riverbed elevations, cell substrate categories, and site discharges were entered into PHABSIM to create hydraulic models for each transect. Hydraulic data were calibrated following procedures in Milhous et al. (1989). We used the calibrated decks for both rivers in IFG4 to simulate hydraulic characteristics for each site at the average flows present during the peak of fall-run chinook salmon spawning for 1989–1996 (Table 4).

Habitat suitability criteria (HSC curves) are used within PHABSIM to translate hydraulic and structural elements of rivers into indices of habitat quality (Bovee 1994). We used the redd measurements from the Merced and Lower American rivers to create stream-specific HSC curves (Gard 1998). We used the HABTAE program and the Merced River specific HSC curves to predict WUA for comparison with the redd locations and densities at 7.79 m^3/s. To calculate total cell WUA, we predicted compound suitability for each cell and multiplied this by the area that each cell represented. The WUA calculated for each cell was summed to produce WUA by transect, and transect WUA at each site was summed to produce site estimates. We also used the HABTAE program and the Merced and Lower American River specific HSC

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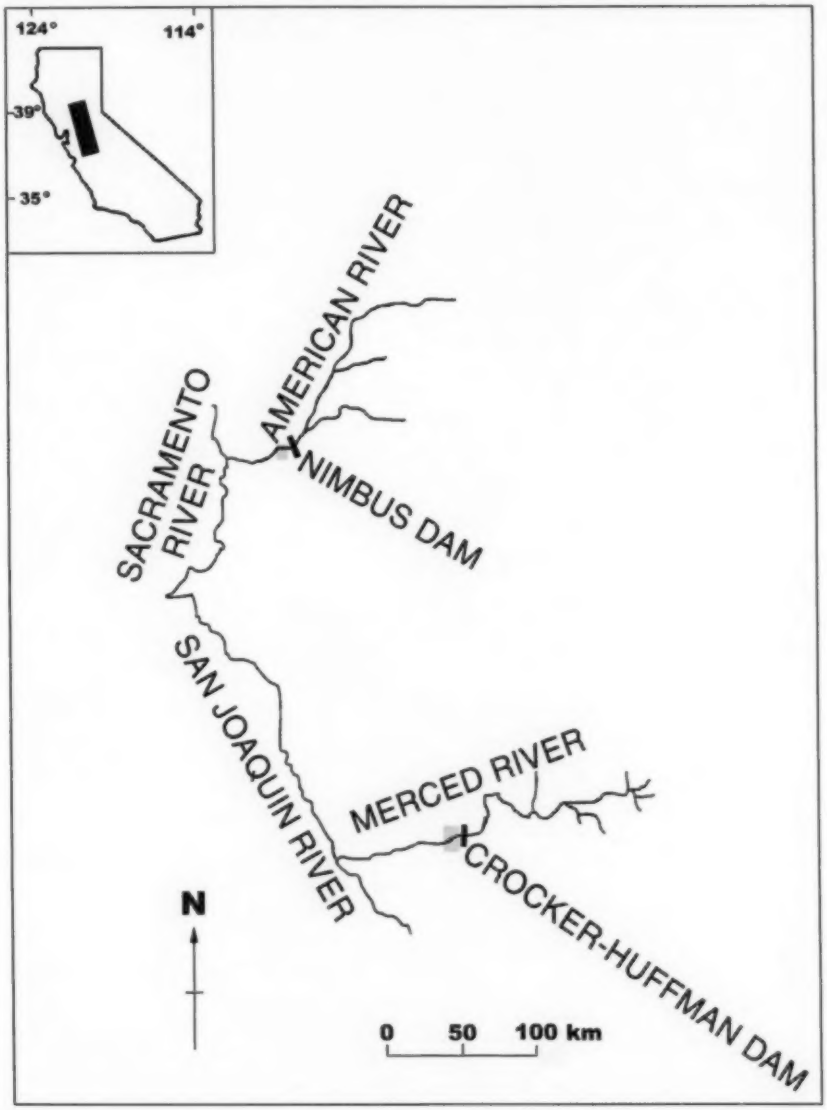
Fig. 1. Location of the Merced and Lower American rivers, California. Shaded areas are the study reaches used to evaluate the relationship between chinook salmon spawning and PHABSIM-predicted habitat index relationships.



curves to predict WUA for each site for the average flows in Table 4.

Data analysis

To examine microhabitat WUA and spawning density correlations for the Merced River in 1996, we compared predicted WUA for each cell along each transect with redd locations and density. We analyzed the data this way for each site and then pooled the entire data set to increase the sample size. We examined the data to determine if, in the cells where we found redds, PHABSIM predicted less WUA than required for a redd, assuming a minimum nest area of 4.5 m^2 (minimum size reported by Burner 1951). If PHABSIM predicted <4.5 m^2 of WUA for a cell containing a redd, we treated the cell as having no WUA. To determine if there was a relationship between chinook salmon spawning density and predicted WUA at the mesohabitat level in the Merced River in 1996, we compared redd density with WUA by transect and by site. Merced River site 1 included two transects that crossed two split channels, and site 2 had two transects crossing three split channels. For the transect-level analysis, the portion of each transect crossing a split channel was treated as a separate transect. All data were compared using the nonparametric gamma correlation coefficient. The gamma statistic is preferable to the Spearman *R* statistic when the data contain many tied observations (Stat Soft, Inc. 1995). The cell-by-cell data had many tied observations.

To examine the relationship between mesohabitat WUA and redd numbers from 1989 through 1996 in the Merced River and from 1991 through 1995 in the Lower American River, we conducted an analysis of covariance (ANCOVA). Redd numbers for the period 1989–1996 were from the California Department of Fish and Game (C. Mayotte, California Department of Fish and Game, Fresno, Calif., unpublished data). The dependant ANCOVA variable was

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Table 2. Average, minimum, maximum, and SD for the number of cells, cell width, cell area, and distance between transects used for PHABSIM data collection and modeling on the Merced and Lower American rivers.

	No. of cells		Cell width (m)		Cell area (m^2)		Distance between transects (m)	
	Merced	American	Merced	American	Merced	American	Merced	American
Average	38	47	1.1	2.6	43.9	278	26.6	34
Minimum	24	34	0.08	0.02	0.08	7.4	11	12
Maximum	58	59	7	11	315.5	1743	77.4	75
SD	8	8.5	0.58	1.4	25.4	237	15.6	20

Table 3. Average, minimum, maximum, and SE for hydraulic characteristics of chinook salmon redds measured in the Merced (n = 186) and Lower American (n = 218) rivers during 1996.

	Depth (m)		Velocity (m/s)		Substrate size (cm)	
	Merced	American	Merced	American	Merced	American
Average	0.4	0.7	0.6	0.7	5–10	5–7.5
Minimum	0.1	0.2	0.14	0.2	2.5–5	2.5–5
Maximum	0.7	1.8	1.26	1.25	10–15	7.5–12.5
SE	0.007	0.02	0.01	0.01	0.18	0.08

number of redds, while the categorical variable was year and the covariate was WUA. Statistical significance was accepted at the 0.05 probability level.

Results

Five of the seven sites on the Merced River during 1996 showed significant relationships between WUA and redd location and density at the microhabitat level (Table 5). Two sites showed no relationship between redd location and simulated WUA at the microhabitat level. When the data for all sites were combined, the relationship between WUA and redd location and density was significant at the microhabitat level (γ = 0.471, P < 0.000001, n = 1060). The PHABSIM predicted zero WUA for 11% of the cells observed to have one or more redds. When we set the WUA equal to zero for cells with <4.5 m^2 of predicted area per redd, 34% of the cells with spawning had zero predicted WUA. With the data thus modified, a significant relationship between cell WUA and redd density and location was still shown (γ = 0.524, P < 0.000001, n = 1060). Ninety-eight percent of cells with no predicted WUA and 90% of the cells with <4.5 m^2 of predicted WUA had no redds.

Mesohabitats with more redds had more WUA. Areas represented by transects with higher WUA had significantly more redds in the Merced River during 1996 (γ = 0.321, P = 0.01, n = 34). Transects with higher predicted WUA had more redds than transects with lower WUA (Table 5). Because Merced River site 1 was very close to the dam and data points from this site were outliers, we excluded it from some analyses. Excluding site 1, the relationship was stronger (γ = 0.495, P = 0.0007, n = 27). At the mesohabitat level (i.e., sites) in the Merced River during 1996, there was a significant relationship between redd density and predicted WUA (γ = 0.714, P = 0.02, n = 7). Excluding site 1, the relationship was again stronger (γ = 0.867, P = 0.01, n = 6).

At the mesohabitat level in the Merced River, we found a significant relationship between the number of redds and WUA (r^2 = 0.17, P = 0.0036, n = 56) (Fig. 2) for the period 1989–1996. Excluding site 1 from the analysis strengthened this relationship (r^2 = 0.38, P = 0.000016, n = 48). Similarly, for the American River at the mesohabitat level for the period 1991–1995, we found a significant relationship between the number of redds observed and WUA (r^2 = 0.40, P = 0.000003, n = 50) (Fig. 3).

Discussion

Shirvell (1989) used regularly spaced transects to examine the relationship between PHABSIM predictions and chinook salmon spawning in Canada and concluded that PHABSIM incorrectly predicted the amount of habitat and locations of chinook salmon spawning. We placed our transects in sites known to be heavily used by spawning salmon and did not space transects uniformly. Rather, transects were spaced so that each transect was representative of the substrate size, riverbed slope, depths, and velocities within the length of river modeled by each transect. We found significant correlations between predicted WUA and chinook salmon spawning at the microhabitat and mesohabitat levels.

In the Merced River, we found a significant relationship between chinook salmon redds and predicted WUA in cells for five of seven sites. The lack of a significant relationship at the other two sites was likely due to low statistical power as a result of the small sample size of redds at these two sites (Table 5). PHABSIM predicted 11% of the cells where we observed redds as unuseable (WUA = 0 initially) and 34% of cells with redds had <4.5 m^2 of WUA. Nonetheless, even though some cells with redds were predicted as having no habitat, cells having WUA were used disproportionately more than cells having no WUA. Since most of the cells with WUA <4.5 m^2 did not have redds, the gamma coefficient was larger when WUA was set to zero for cells with WUA <4.5 m^2. Nineteen of the 39 cells where spawning was observed in habitat predicted as unuseable by PHABSIM had unsuitable substrate (i.e., too large or aquatic vegetation). The PHABSIM model simulates habitat for an area of river based on data collected along a transect perpendicular to the river. Substrate is variable within a streambed, and simply estimating it at a point may not accurately capture its char-

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Table 4. Time period, average, minimum, maximum, and SE for daily average chinook salmon spawning river discharge (m^3/s) in the Merced and Lower American rivers.

	1989	1990	1991	1992	1993	1994	1995	1996
Merced								
Time period	22 Nov. – 31 Dec.	20 Nov. – 27 Dec.	14 Nov. – 31 Dec.	4 Nov. – 23 Dec.	26 Oct. – 17 Nov.	8–20 Nov.	24 Oct. – 7 Nov.	23 Oct. – 14 Nov.
Average	5.7	6.0	7.2	6.9	6.2	6.7	12.9	8.4
Minimum	5.4	5.4	6.9	6.1	5.4	6.0	11.0	7.6
Maximum	6.1	6.6	7.3	10.3	7.5	7.3	13.8	9.0
SE	0.03	0.04	0.02	0.2	0.1	0.1	0.2	0.1
American								
Time period	—	—	19 Oct. – 25 Nov.	3 Nov. – 4 Dec.	28 Oct. – 16 Nov.	27 Oct. – 16 Nov.	16 Oct. – 28 Nov.	—
Average	—	—	41.8	16.1	55.6	32.7	68.8	—
Minimum	—	—	27.3	14.9	49.6	19.2	66.5	—
Maximum	—	—	92.6	18.6	61.7	39.9	72.2	—
SE	—	—	0.5	0.02	0.2	0.5	0.03	—

Note: Redd count data were not available for 1989, 1990, and 1996 for the Lower American River.

acteristics between transects. Sampling above and below the transect in the cells to be represented by PHABSIM might improve the accuracy of the substrate component of predicted spawning habitat.

For the other instances where spawning occurred in cells that PHABSIM predicted as having little or no WUA, the absence of WUA was due to high predicted velocities (11 cells) or low depth (nine cells). Higher velocities have lower suitabilities, and in the calculation of WUA, cells with low HSC values for velocity have lower overall WUA predictions. We measured mean column velocities at redds of up to 124 cm/s, yet the criteria curves give this a low suitability value due to the infrequent occurrence of this velocity in our redd measurements. Of the cases where PHABSIM predicted no habitat due to depths with low suitability, two redds were in cells with depths <12 cm, the lowest depth at which we observed salmon spawning (Table 3). The others were due to the low HSC values for shallow depths, resulting in PHABSIM calculating lower habitat, similar to as discussed above for velocity.

Fish spawning in areas predicted as having little or no WUA based on PHABSIM-predicted depth or velocity may be due to (*i*) inaccuracies in PHABSIM's prediction of depths or velocities, (*ii*) variation in depth and velocity in a cell along the stream profile, (*iii*) saturated habitat conditions, (*iv*) chinook salmon spawning habitat being composed of more than depth, velocity, and substrate, or (*v*) low compound suitability of a cell. DeVries (1997) suggested that changes in bed topography due to repeated heavy spawning cause hydraulics in these areas to become quite complicated. Use of two-dimensional hydraulic and habitat models (Leclerc et al. 1995) may help address inaccuracies in habitat predictions resulting from complex hydraulics and from longitudinal variation in depth, velocity, and substrate. Vaux (1968) suggested that upwelling, associated with a concave streambed profile, is an important feature of chinook salmon spawning habitat. The PHABSIM cannot simulate these features. Vyverberg et al. (1996) found that substrate permeability was an important indicator of chinook salmon spawning use. We indirectly addressed permeability by only locating transects in high spawning use areas. Permeability could be directly addressed in PHABSIM by including it as a component of substrate. This would require measuring permeability at redd locations during criteria development and along transects.

An apparent lack of sufficient habitat resulting from low compound suitability is a result of treating WUA as the actual area of streambed available for spawning at a small scale. For example, a 5-m^2 area of stream with a compound suitability of 0.2 would have a WUA value of 1.0 m^2 and might be considered unsuitable, even though the area is used at a low frequency. In this case the calculated WUA may be interpreted as that, on average, two out of 10 such areas will have a redd. In contrast, an area of 1 m^2 with a compound suitability of 1.0 would also have a WUA of 1.0 m^2 and would also be considered unsuitable, and in fact is unsuitable, as the total area is <4.5 m^2. At a larger scale (i.e., at the transect or mesohabitat level) the areas with low compound suitability are combined such that the total number of redds corresponds to total WUA. Consistent with this conclusion, our results showed that the relationship between number of redds and WUA increased in strength with increased scale (i.e., the relationship at the mesohabitat level was stronger than at the transect and cell levels). Thus, at larger scales, WUA may be a good predictor of available spawning habitat.

The results of our analysis of Merced River data at the transect and mesohabitat levels for 1996 (Table 5) and for multiple years (Fig. 2) suggested that the proximity of a site to the upstream limit for chinook salmon migration influences spawning numbers. Specifically, Merced River site 1 was located 0.2 km downstream of Crocker–Huffman Dam and had very high spawning levels, relative to the amount of WUA at the site. The aggregation of chinook salmon below this barrier increased the density of spawning above that which was expected based on the amount of WUA available. We observed redd superposition at this site and very little redd superposition at the other sites on the Merced River during 1996. The aggregation of chinook salmon below the dam lowered the ability of PHABSIM to predict the amount of spawning at this site, and thus the relationship between the number of redds and WUA was stronger when this site

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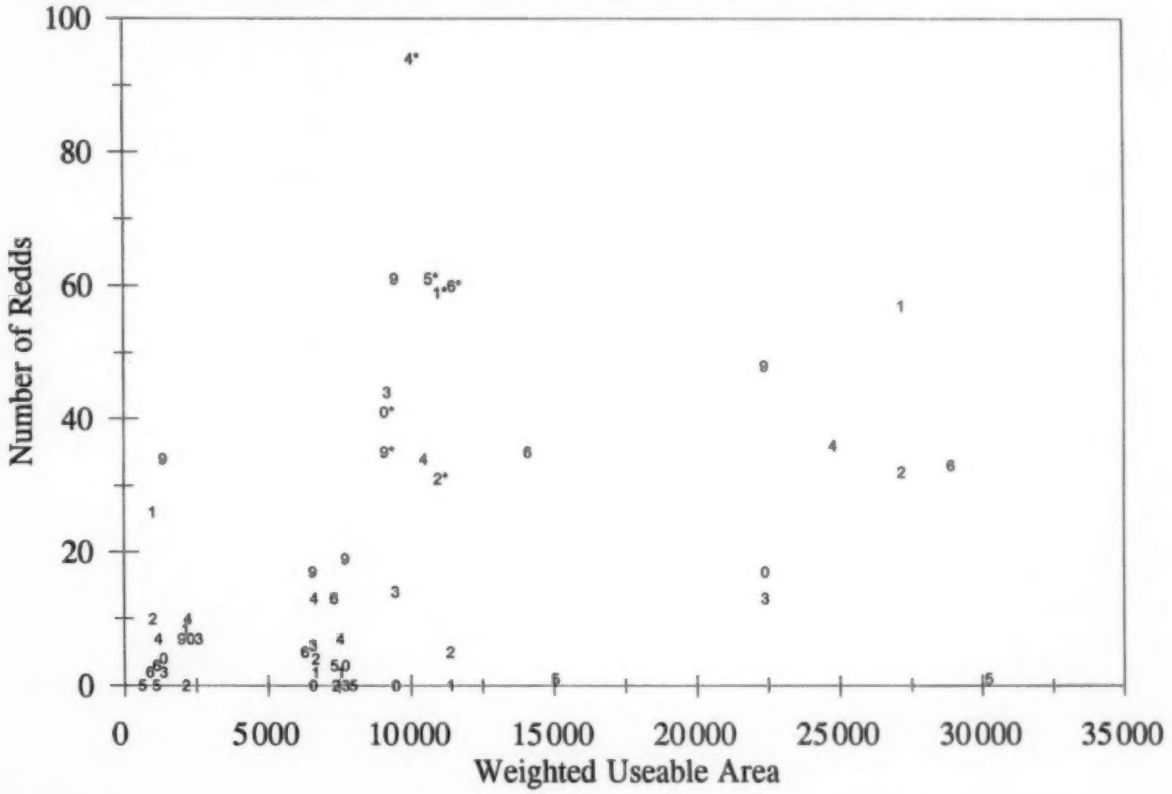
Table 5. Merced River study site summary for 1996.

Site	Riffle area (m^2)	WUA (m^2)	No. of redds	γ cell WUA	*P*
1	4224.3	338.3	60	0.244	<0.02
2	6471.5	412.0	35	0.383	<0.001
3	1236.4	33.1	3	0.05	>0.50
4	980.7	26.2	2	0.03	>0.50
5	7402.2	844.4	33	0.166	<0.001
6	6547.1	214.1	13	0.329	<0.01
7	4061.7	184.3	5	0.189	<0.02

Note: Riffle area and WUA are calculated at a discharge of 7.79 m^3/s. γ cell WUA and *P* values are gamma correlation coefficients and statistical significance of the coefficient for relationships between redd location and WUA at each site on a cell-by-cell basis. Number of redds was the number used in the transect- and site-level analyses. Only 55 redds were used for site 1 in the cell-level analyses because we were unable to determine from our field data in which cell five of the redds were found, although we were able to determine in which transect they were.

Fig. 2. Redd numbers versus WUA for seven sites on the Merced River from 1989 to 1996. Asterisks indicate site 1. Numbers are the last digit of the year of the data (i.e., 9's are data from 1989, 1's are data from 1991, etc.).



was excluded from the analysis. We did not observe this effect in the American River, either because the most upstream site was 1.5 km below the dam or because the effect was obscured because the most upstream site had the highest WUA.

Kondolf et al. (1996) evaluated the spawning gravel enhancement of the Merced riffle site 1 and found that gravels placed in this riffle were scoured out every 1.5 years and that the benefit to spawning salmon was questionable. Gravels were placed in this site again in 1996 prior to fall-run spawning (M. Cozart, California Department of Fish and Game, Merced River Hatchery). The placement of spawning gravels did not increase the available WUA above that of all other riffles (Table 5). Yet this may have influenced spawning, as all the gravels were fresh and clean. The amount of fine material in the substrate and the porosity of spawning gravels could be included in PHABSIM WUA calculations by incorporating them into the substrate component of habitat.

Conder and Annear (1987) stated that if habitat variables modeled by PHABSIM exhibit a strong influence on standing crop, WUA–density relationships may be valid. DeVries

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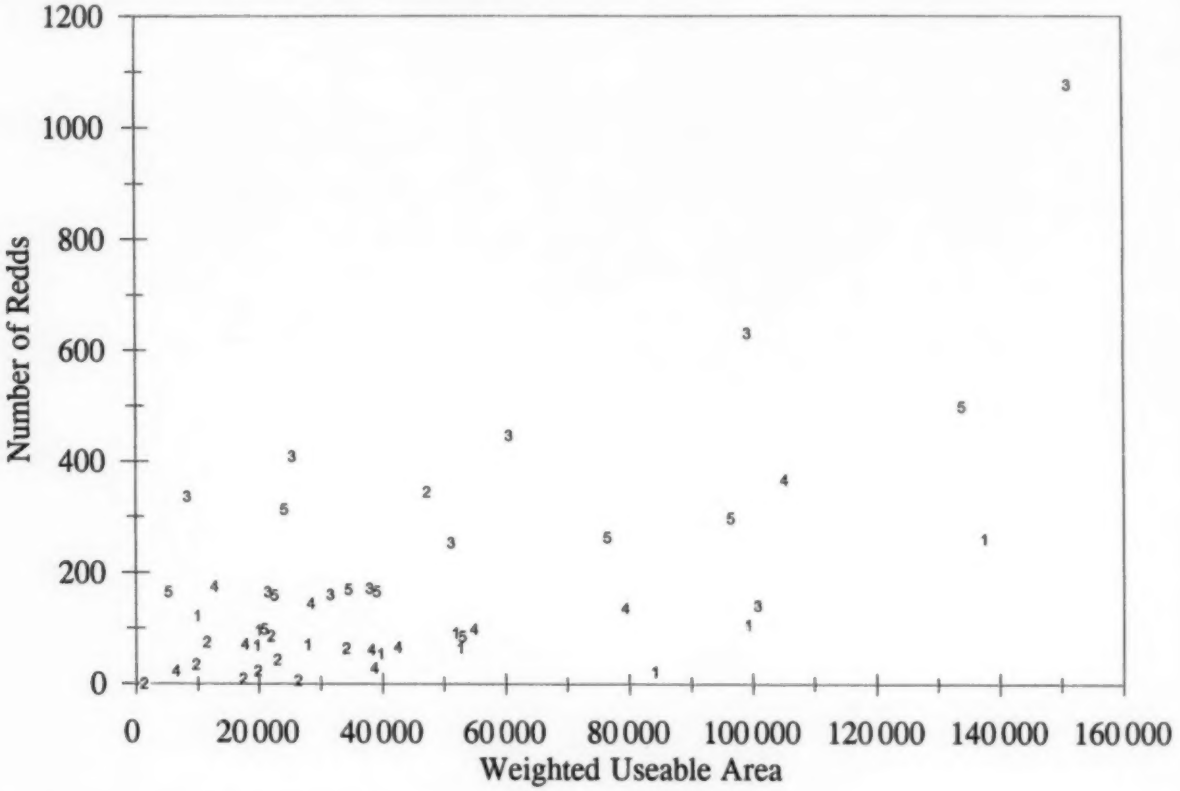
Fig. 3. Redd numbers versus WUA for 10 sites on the Lower American River from 1991 to 1995. Numbers are the last digit of the year of the data (i.e., 9's are data from 1989, 1's are data from 1991, etc.).



(1997) stated that substrate followed by velocity are the most influential hydraulic and geomorphic features influencing spawning. For chinook salmon spawning in the Merced and Lower American rivers, depth, velocity, and substrate appear to be important habitat factors. Attempting to predict flow habitat induced chinook salmon population responses is complicated because much of their life is not spent in rivers. The positive correlations between flow-related WUA estimates and chinook salmon redds indicated by most of our results suggest that fish may respond to flow-related hydraulic improvements. However, without set flows and long-term monitoring, the effects of flow alterations on salmon populations in the Merced and Lower American rivers will remain unknown.

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Analysis of straying variation in Alaskan hatchery chinook salmon (*Oncorhynchus tshawytscha*) following transplantation

Jeffrey J. Hard and William R. Heard

Abstract: In 1976 chinook salmon (*Oncorhynchus tshawytscha*) gametes from the Chickamin and Unuk rivers in southeastern Alaska were transplanted 250 km to establish hatchery runs at Little Port Walter (LPW), Baranof Island. From 1977 to 1989, 1 862 058 marked smolts from 12 broods were released from LPW. Homing and straying were estimated from adult recoveries at 25 locations in Alaska and British Columbia between 1981 and 1989. Of 22 198 LPW fish recovered over this period, 21 934 (98.8%) were collected at LPW. Of 264 fish recovered elsewhere, 38.3% were within 7 km of LPW; 64.4% were within 25 km of LPW. No LPW fish were recovered from the ancestral rivers, but nine fish were recovered from rivers supporting wild chinook salmon. Straying declined with distance from the release site but varied between hatcheries and streams. Straying declined with increasing age and run size. Straying was similar between the populations but varied among broods, and analysis of straying in experimental groups provided evidence for a heritable component. Males strayed more often than females. Population, gender, run size, and recovery age interacted to produce substantial variation in straying, indicating that run composition can produce complex straying responses.

Résumé : En 1976, des gamètes de quinnat (*Oncorhynchus tshawytscha*) des rivières Chickamin et Unuk (sud-est de l'Alaska) ont été transplantées à 250 km à Little Port Walter (LPW, sur l'île Baranof) pour y établir des remontes de saumons d'élevage. De 1977 à 1989, 1 862 058 smolts marqués issus de 12 cheptels de géniteurs ont été lâchés à LPW. Le retour aux frayères natales et le vagabondage ont été estimés à partir de récupérations d'adultes à 25 endroits en Alaska et en Colombie-Britannique entre 1981 et 1989. Sur les 22 198 poissons de LPW recapturés durant cette période, 21 934 (98,8%) l'ont été à LPW. Sur les 264 poissons recapturés ailleurs, 38,3% l'ont été à moins de 7 km de LPW et 64,4% à moins de 25 km de LPW. Aucun poisson de LPW n'a été recapturé dans les rivières ancestrales, mais neuf poissons ont été recapturés dans des rivières fréquentées par des quinnats sauvages. Plus on s'éloignait du site de lâcher, moins le vagabondage était important, mais il variait selon les écloseries et les cours d'eau. Plus l'âge était élevé et plus la taille de la remonte était importante, plus le vagabondage diminuait. Le vagabondage était similaire d'une population à l'autre, mais variait selon les cheptels de géniteurs; par ailleurs, l'analyse du vagabondage dans des groupes expérimentaux a montré que ce comportement avait une composante héréditaire. Les mâles vagabondaient plus souvent que les femelles. Population, sexe, taille de la remonte et âge à la recapture interagissaient pour produire une variation substantielle dans le vagabondage, ce qui montre que la composition de la remonte peut entraîner des modalités de vagabondage complexes.

[Traduit par la Rédaction]

Introduction

A cornerstone of Pacific salmon (*Oncorhynchus* spp.) biology is that adult salmon return from the sea to spawn in their natal stream, providing a mechanism for reproductive isolation and adaptive divergence among populations (Ricker 1972). Although the navigational cues that salmon use during oceanic migration are not well understood (Royce et al. 1968; Quinn and Groot 1984), it is now widely believed that olfactory cues help to guide them to the natal stream during the final stages of migration (Cooper et al. 1976; Hasler et al. 1978; Dittman et al. 1996). Salmon have been shown to "imprint" to marine as well as freshwater release sites (Mahnken and Joyner 1973; Sutterlin et al. 1982). Because the coupling of smoltification and imprinting with seaward migration may be necessary for precise homing (Heard 1996), releases of hatchery fish that disrupt or circumvent the coupling of these processes may reduce homing ability.

Straying is adaptive if it results in colonization of suitable freshwater habitats or helps adults to avoid unfavorable conditions at the spawning or rearing site. Detectable straying is often infrequent, however, even in salmon transplanted to unfamiliar areas (Donaldson and Allen 1958; Jensen and Duncan 1971). Adaptations to ecologically distinctive habitats may restrict the success of straying fish. In hatchery fish, straying is highly variable and depends on fish release

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practices (Unwin and Quinn 1993; Pascual et al. 1995) as well as stock origin (McIsaac and Quinn 1988). The degree of straying may depend on environmental factors at the spawning site but also characteristics of the returning adult population, including fish age, run size, and return timing (Quinn and Fresh 1984; Quinn et al. 1991; Labelle 1992; Unwin and Quinn 1993).

In this paper, we estimate homing and straying in two populations of chinook salmon (*Oncorhynchus tshawytscha*) established by transplanting gametes from two wild Alaskan populations to a remote research hatchery located 150 km from any streams known to support chinook salmon. Fewer than 40 of the 2000 watersheds that exist in southeastern Alaska appear to support chinook salmon, and most of the major spawning grounds are widely separated (Heard et al. 1995). Gharrett et al. (1987) showed that chinook salmon populations in this region were genetically more heterogeneous than those elsewhere in Alaska and argued that temporally stable genetic differences reflect low gene flow among these populations. However, homing and straying of Alaskan chinook salmon are poorly documented, and recently established hatchery programs for chinook salmon in this region pose a threat to locally adapted wild populations if hatchery fish stray into and reproduce successfully in these systems (Hindar et al. 1991; Heard et al. 1995). Careful selection of hatchery locations, broodstocks, and production characteristics might help to minimize opportunities for straying into wild systems.

In evaluating variation in homing and straying of Little Port Walter (LPW) chinook salmon over 9 years following transplantation, we examine spatial patterns of straying to assess the opportunities that these fish had to interact with spawning wild fish. We then test the null hypothesis that run characteristics, including broodstock source, brood year, duration of marine residence, number of returning adults, gender, and age at release, had no detectable effects on straying of the transplanted fish.

Materials and methods

Study site

Stream-type chinook salmon have been cultured since 1976 at the National Marine Fisheries Service research station at LPW on Baranof Island in southeastern Alaska (Fig. 1). Chinook salmon were established at LPW to develop broodstocks for use in southeastern Alaska hatcheries, to support enhancement research for this species in Alaska, and to augment harvest in Alaskan commercial and recreational fisheries. Sashin Creek, which drains a 1340-ha watershed and is the source of culture water for the station, flows into the west end of LPW on the southeastern coast of Baranof Island. Sashin Creek does not support chinook salmon, although endemic runs of pink salmon (*Oncorhynchus gorbuscha*), chum salmon (*Oncorhynchus keta*), coho salmon (*Oncorhynchus kisutch*), steelhead (*Oncorhynchus mykiss*), and Dolly Varden (*Salvelinus malma*) spawn in Sashin Creek. Pink salmon are the most abundant of these species, with an annual mean of about 29 000 spawners (Vallion et al. 1981). The Sashin Creek watershed also supports rainbow trout (*O. mykiss*) and coastrange sculpin (*Cottus aleuticus*). The isolation of Sashin Creek from wild chinook salmon populations and the presence of the research facility were primary reasons for establishing the chinook salmon populations there: it was thought that siting the program at LPW would limit opportunities for interactions with wild conspecifics (Heard et al. 1995). The watersheds nearest LPW that support endemic runs of chinook salmon are the Farragut River, a mainland system 150 km northeast of LPW, and King Salmon River, a system on Admiralty Island 220 km north of LPW (Fig. 1).

In 1976, eggs and milt were taken from adults in the Chickamin and Unuk rivers on Behm Canal, southeastern Alaska (Fig. 1). The unmixed gametes were transported 250 km northwest to LPW, where they were combined and the resulting young cultured to the smolt stage. Gametes were also transplanted to LPW from the Unuk River each year from 1977 to 1981. Fish from the two populations were incubated and reared separately; culture details are described in Hard et al. (1985). Beginning with the 1982 brood, all chinook salmon smolts released from LPW were progeny of adults that returned there. All smolts released from LPW were liberated directly from floating vertical raceways into the estuary or transferred from the raceways to marine net pens, from which they were released. Most yearlings were released in May; subyearlings were released in September or October.

Straying assessment

We evaluated recoveries of adult LPW chinook salmon from 1981 through 1989. Returns before 1981 were composed almost exclusively of males; these returns were not considered in our analysis because straying was not assessed in those years. Data are available from all age groups of four broods (1979–1982) of Unuk River and two broods (1981 and 1982) of Chickamin River chinook salmon. Additional information is available on some age groups for other broods released from LPW, including seven broods from the Unuk River (1976–1978 and 1984–1987) and three from the Chickamin River (1976, 1986, and 1987).

Over 1.8 million smolts were released from LPW from the 1976–1987 broods (Table 1); all were marked with coded-wire tags, permitting us to determine the origin and culture history of each fish recovered. The majority (69%) of these smolts were Unuk River fish liberated as yearlings after about 650 days of freshwater culture. Most of the remainder were Unuk River subyearlings or Chickamin River yearlings (Table 1). All fish in the LPW release groups considered in this paper were marked; no expansions for tagging rates were necessary. Tag shedding rates generally ranged from 0 to 5%, with a few tagged groups (each tagged group of fish was from a single brood and had common culture and release characteristics) having values as high as 40% (mean ± 2 SE = 2.8 ± 1.0%, n = 266 tagged groups).

Maturing chinook salmon that returned to LPW were captured daily or every few days in July and August and periodically thereafter until mid-September of each year at a permanent weir at the mouth of Sashin Creek. Most fish were captured in the estuary immediately below the weir with a large seine that entrapped fish when they attempted to access the creek on a flooding tide. The Sashin Creek weir prevented any chinook salmon from entering the stream. Chinook salmon that strayed from the release site were recovered during surveys of several hatcheries, rivers, and streams in southeastern Alaska and British Columbia (Fig. 1). Recoveries were made with hatchery fences, weirs, fish wheels, spear guns, beach seines, or snagging gear, and all captured fish were examined for coded-wire tags.

Streams sampled most frequently, from one to three or more times weekly during each annual run, were within 25 km of LPW and were concentrated in the Port Walter drainage. Port Walter streams nearest LPW (Borodino Lake Creek, Lovers' Cove Creek, and Osprey Lake Creek) were sampled up to five times weekly. More distant streams on Baranof Island, other islands, and the mainland were surveyed periodically by foot or during routine operation of weirs, hatchery fences, and other research activities. We removed heads from carcasses of adults that we killed in remote streams after collecting size data.

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Fig. 1. Southeastern Alaska and the Queen Charlotte Islands, British Columbia, showing numbered locations where LPW chinook salmon were recovered from 1981 to 1989. H, hatchery; S, stream; W, weir. Squares represent sites where weirs were operated during this period, but where no LPW chinook salmon were recovered. 1, LPW (H); 2, Osprey Lake Creek (S); 3, Lovers' Cove Creek (S); 4, Borodino Lake Creek (S); 5, Port Armstrong (H); 6, Banner Lake Creek (W); 7, Parry Creek (S); 8, Gut Bay Creek (S); 9, Falls Lake Creek (W); 10, Redoubt Lake Creek (W); 11, Sheldon Jackson (H); 12, Hidden Falls (H); 13, Politofski Lake Creek (W); 14, Farragut River (S); 15, Karta River (W); 16, Crystal Lake (H); 17, Crescent Lake (W); 18, Naha River (S); 19, Stikine River (S); 20, Port Snettisham (H); 21, Deer Mountain (H); 22, Whitman Lake (H); 23, Taku River (S); 24, Yakoun River (H); 25, Pallant Creek (H).

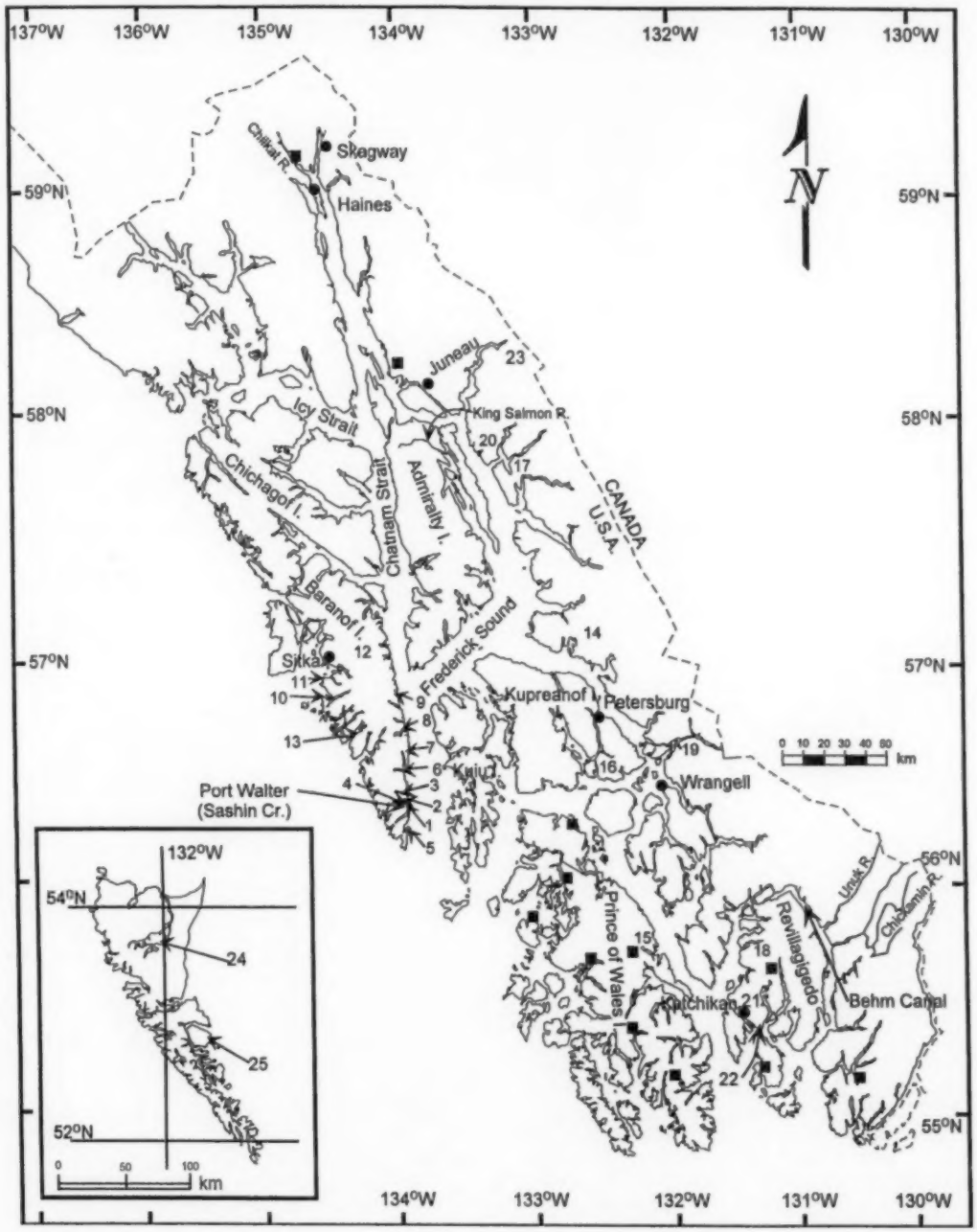

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Table 1. Releases of stream-type chinook salmon from LPW, southeastern Alaska, between 1977 and 1989.

Brood year	Release year	Population	No. of fish released to sea	
			Subyearling	Yearling
1976	1977–1978	Chickamin	4 978	13 397
1976	1978	Unuk	—	22 508
1977	1978–1979	Unuk	55 388	46 390
1978	1979–1980	Unuk	22 689	156 921
1979	1981	Unuk	—	27 303
1980	1982	Unuk	—	20 166
1981	1983	Chickamin	—	25 630
1981	1983	Unuk	—	93 456
1982	1984	Chickamin	—	43 242
1982	1984	Unuk	—	130 085
1983	1985	Unuk	—	165 839
1984	1986	Unuk	—	203 961
1985	1986–1987	Unuk	92 092	210 712
1986	1987–1988	Unuk	46 297	141 104
1986	1987–1988	Chickamin	43 607	145 211
1987	1989	Unuk	—	58 494
1987	1989	Chickamin	—	86 588
Total			271 051	1 591 007

Note: The two broodstock sources are located in southern southeastern Alaska. All fish were marked with an excised adipose fin and coded-wire tag.

Table 2. Recoveries of marked maturing chinook salmon on or near nonnatal spawning grounds from 1981 to 1989 in relation to distance from the LPW release site.

Distance from release site (km)	Sites surveyed	No. of fish recovered			
		H	W	S	Total
0–25	6	55	14	101	170
26–50	3	0	10	6	16
51–100	6	41	0	0	41
101–200	10	14	4	6 (6)	24
201–300	10	5	0	6 (3)	11
>300	2	2	0	0	2
Total	40	117	28	119 (9)	264

Note: Sites surveyed reflect the average number of sytems examined in that distance category. H, hatchery; W, weir not at a hatchery; S, stream recovery. Parentheses indicate recoveries from wild chinook salmon streams.

During this study, chinook salmon were examined at a total of 40 systems in Alaska and British Columbia; 26 of these systems had weirs or hatchery fences operated by cooperating National Marine Fisheries Service, Alaska Department of Fish and Game, Regional Aquaculture Association, and Canadian hatchery personnel (Table 2; Fig. 1). Surveys of systems with weirs were typically conducted regularly by staff on site, but surveys of most other sites were irregular and weather dependent. Of the 26 streams with weirs surveyed, seven were on Prince of Wales Island in 1982 and 1983, but no LPW chinook salmon were recovered there in those years (Eiler et al. 1984); these streams were not surveyed for chinook salmon after 1983. Nine streams without weirs were also surveyed over these years (but not in all years); six of these streams were >25 km away from LPW.

Statistical analyses

For tests of the effects of individual factors on straying, we used the likelihood ratio (G) test; each test statistic was corrected for bias in type I error. Relationships between straying frequency and run size were evaluated with geometric mean regression (Ricker 1984) because these variables have similar coefficients of variation (70–106%). The arcsine transformation was applied to straying frequencies before regression analysis because straying frequencies were typically low.

We used log-linear models to evaluate the effects of interactions among five categorical factors on straying frequency. This multivariate procedure analyzes factor associations to construct models of factor combinations that adequately explain the data. Preliminary analyses indicated substantial variation in straying among all ages at return and among run sizes, but it was not possible to fit unique solutions to the data because of the large proportion of empty cells. Therefore, pooling of categories for both age at return and run size was necessary. The form of the saturated model was

$$(1)\quad \ln \hat{f}_{ijklm} = \mu + P_i + G_j + A_k + N_l + D_m + PG_{ij} + PA_{ik} + \ldots + PGA_{ijk} + PGN_{ijl} + \ldots + PGAN_{ijkl} + PGAD_{ijkm} + \ldots + PGAND_{ijklm}$$

where $\hat{f}$ is the expected straying frequency in cell $ijklm$ of the five-way contingency table, μ is the overall mean of the logarithms of expected cell frequencies, P_i is the effect of population i (P_1 = Unuk, P_2 = Chickamin), G_j is the main effect of gender j, A_k is the effect of age at recovery category k (A_1 <5 years, $A_2 \geq 5$ years), N is the effect of escapement category l ($N_1 \leq 1000$, $N_2 > 1000$), D is the recovery disposition m of each fish (homing or straying), $PG_{ij} + PA_{ik} + \ldots$ denotes the 10 first-order interactions among pairs of these factors, $PGA_{ijk} + PGN_{ijl} + \ldots$ denotes the 10 second-order interactions among groups of three of the factors, $PGAN_{ijkl} + PGAD_{ijkm} + \ldots$ denotes the five third-order interactions among groups of four of the factors, and the term $PGAND_{ijklm}$ is the single fourth-order interaction among all the factors. Fit of smaller models to the observed data was determined by testing the fit of each model with the likelihood ratio χ^2, removing specific terms from the model, and testing the significance of the differences in χ^2 that resulted. In addition, Raftery's Bayesian information criterion (BIC) was used to compare the fit of simpler models with that of

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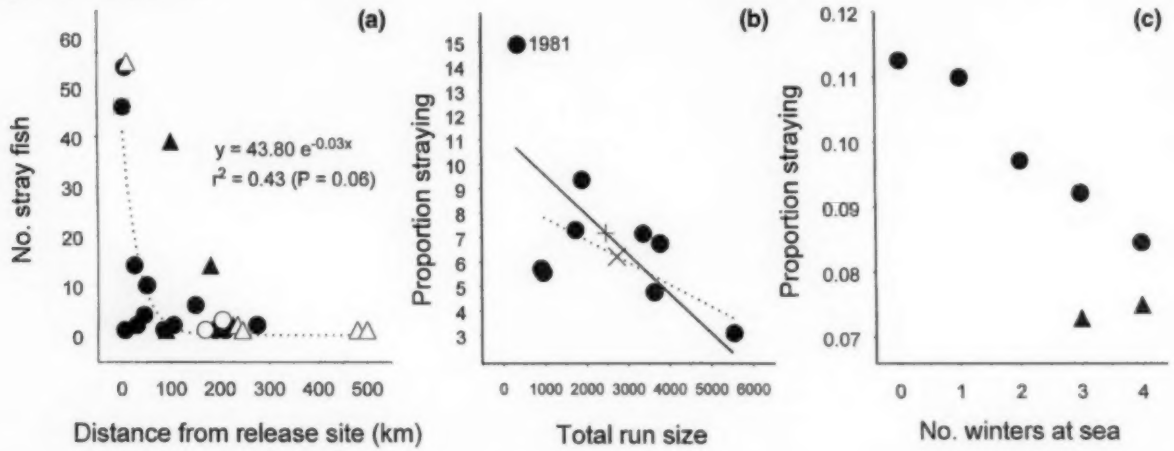
Fig. 2. (*a*) Variation in recoveries of LPW chinook salmon with distance from the release site for all years combined (1981–1989). Solid symbols represent recoveries north of LPW; open symbols represent those south of LPW. Triangles represent hatchery recoveries; circles represent recoveries made away from hatcheries. The dotted line represents an exponential decay model that best fits the data. (*b*) Central trend lines (Ricker 1984) for estimated straying rate in LPW chinook salmon as a function of total run size for the 1981–1989 returns (solid line) and for those excluding 1981 (dotted line). For each line, the upper 95% confidence limit does not include zero. The + and × denote the joint sample means for the 1981–1989 and 1982–1989 data sets, respectively. Proportions are arcsine square-root transformed. (*c*) Relationship between straying rate and adult age, measured as the number of winters spent at sea, for annual population-specific returns of >50 fish. Circles represent data from Unuk River fish; triangles represent data from Chickamin River fish. The regression for Unuk River is significantly negative ($y = 0.114 - 0.007x$; $r^2 = 0.97$, $P < 0.005$); the regression for the combined data is significantly negative as well ($y = 0.115 - 0.009x$; $r^2 = 0.79$, $P < 0.01$). Proportions are arcsine square-root transformed.



the more complex model. The BIC is a likelihood ratio χ^2 adjusted for both the degrees of freedom in the model and the sample size. For all tests, the experimentwise significance level was $P < 0.05$.

Results

Spatial straying variation

An estimated 16 139 chinook salmon released from LPW were harvested in southeastern Alaska commercial and recreational fisheries between 1981 and 1989 (McGee et al. 1990). An additional 22 198 maturing fish were recovered during the same period at or near the release site or other potential spawning areas. Most of these fish (21 934) were recovered at the release site; 264 (1.2%) were recovered at 24 other locations ranging from <5 to >500 km from LPW (Fig. 1; Table 2). Thirty-eight percent of the fish recovered away from LPW (101 fish) were recovered in Port Walter streams within 7 km of LPW; 64% (170 fish) were captured within 25 km (Table 2).

Chinook salmon released from LPW were recovered at several locations where weirs or hatcheries were operated, including weirs at Banner Lake and Falls Lake and hatcheries at Port Armstrong, Hidden Falls, and Crystal Lake (Fig. 1). No LPW chinook salmon were recovered from the two ancestral Behm Canal rivers during annual spawner surveys there. However, 11 LPW fish were recovered from mainland streams at least 130 km from LPW; nine of these were from river systems with natural runs of chinook salmon. Two LPW chinook salmon were recovered from the Politofski Lake outlet stream on the west coast of Baranof Island, and two were recovered from Canadian hatcheries in the Queen Charlotte Islands (Fig. 1). Of all the LPW strays recovered from 1981 to 1989, 159 (60.2%) were recovered from systems without native chinook salmon.

When combined for all groups over all years of data, the numbers of LPW chinook salmon recovered showed a steep decline with distance from the release site (Fig. 2*a*). An exponential decay model based on least squares provided the best fit to the data: $y = 43.80e^{-0.03x}$. The fit to the model was poor ($r^2 = 0.43$, $P = 0.06$) but was a substantial improvement upon the fit of a linear model ($r^2 = 0.22$). The poor fit to the exponential model largely reflects higher than expected recoveries of LPW fish at two hatcheries within 200 km of LPW (solid triangles above the regression line in Fig. 2*a*) and fewer than expected recoveries in one Port Walter stream, Lovers' Cove Creek (the lowermost solid circle in Fig. 2*a*).

Effect of recovery method and location

The numbers of stray fish recovered varied significantly ($P < 0.001$) among types of recovery sites (hatchery, weir, or stream without weir) for three different categories of distance from the release site (≤ 25, 26–100, and >100 km) ($G = 46.71$, 4 df). Across these distance categories, recoveries of fish varied between streams and hatcheries or weirs ($G \geq 17.77$, 1 df, $P < 0.001$) but not between hatcheries and weirs ($G = 0.22$, 1 df, $P > 0.50$). For sites >25 km away from LPW, recoveries were more frequent in streams than at hatcheries or weirs ($G = 6.72$, 1 df, $P < 0.01$). These results indicate a strong interaction between recovery of stray fish

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Table 3. Homing and straying of marked maturing chinook salmon released from LPW in relation to brood year.

	Subyearling releases			Yearling releases		
Brood year	Homing	Straying	Total	Homing	Straying	Total
Chickamin River stock						
1976	6 (85.7)	1 (14.3)	7	150 (94.4)	11 (5.6)	161
1981	—	—	—	737 (99.9)	1 (0.1)	738
1982	—	—	—	599 (98.7)	8 (1.3)	607
1986	—	—	—	55 (91.7)	5 (8.3)	60
1987	—	—	—	126 (93.3)	9 (6.7)	135
Total	6 (85.7)	1 (14.3)	7	1 667 (98.0)	34 (2.0)	1 701
Unuk River stock						
1976	—	—	—	146 (94.8)	8 (5.2)	154
1977	22 (95.6)	1 (4.4)	23	96 (98.9)	1 (1.1)	97
1978	22 (95.6)	1 (4.4)	23	909 (97.5)	23 (2.5)	932
1979	—	—	—	1 797 (98.4)	28 (1.6)	1 795
1980	—	—	—	414 (98.3)	7 (1.7)	421
1981	—	—	—	3 299 (99.4)	20 (0.6)	3 319
1982	—	—	—	6 639 (99.1)	60 (0.9)	6 699
1983	—	—	—	3 730 (99.1)	35 (0.9)	3 765
1984	—	—	—	1 980 (99.4)	11 (0.6)	1 991
1985	129 (99.2)	1 (0.8)	130	641 (98.5)	10 (1.5)	651
1986	20 (95.2)	1 (4.8)	21	131 (97.8)	3 (2.2)	134
1987	—	—	—	316 (94.3)	19 (5.7)	335
Total	193 (98.0)	4 (2.0)	197	20 068 (98.9)	225 (1.1)	20 293

Note: Data include incomplete returns for certain age groups from 1976–1978 and 1984–1987 broods and complete returns for 1979–1983 broods. Percentages are in parentheses.

at different types of sites and the distance of the recovery site from the release location; most of the variation is due to fewer than expected recoveries of strays from distant streams and higher than expected recoveries from nearby hatcheries.

Effects of population, culture environment, run size, and life history

We detected no significant differences in straying between Unuk and Chickamin River stock fish when compared either among four complete broods ($G = 1.05$, 1 df, $P > 0.10$) or between two comparable releases of 1981 and 1982 brood fish only ($G = 0.26$, 1 df, $P > 0.50$). Among all fish recovered during 1981–1989, Chickamin River fish strayed at twice the rate of Unuk River fish (2.1 versus 1.0%; $G = 194.8$, 16 df, $P < 0.0001$), but these data included fish from several broods of both stocks for which returns are incomplete. Of the five broods of LPW chinook salmon for which returns of all ages are complete (1979–1983), the frequency of strays recovered was highest in 1979 brood Unuk River (1.6%) and 1982 brood Chickamin River (1.3%) fish. No subyearling releases were made from these broods in either population (Table 3); for other broods of Unuk River fish only, subyearling fish showed no tendency ($P > 0.90$) to stray at higher frequencies than yearlings ($G < 0.01$, 1 df), but the power of this test is low. For both stocks, straying varied significantly among complete brood years (Unuk: $G = 12.36$, 4 df, $P < 0.025$; Chickamin: $G = 7.29$, 1 df, $P < 0.01$).

The relative frequency of strays recovered declined with increasing run size (Fig. 2*b*). This relationship was also significant ($P < 0.05$) when excluding data from 1981, when recoveries of fish away from the release site were high for a numerically small run. Recovery of adult chinook salmon at the Sashin Creek weir in 1981 was hindered by extremely low stream discharge (<0.2 $m^3 \cdot s^{-1}$), which may have caused the adult chinook salmon to seek other nearby streams without barriers or with greater discharge. Recoveries made by seining downstream from the weir were also delayed in 1981 compared with efforts in subsequent years. Sixteen of 23 LPW chinook salmon recovered away from the release site in 1981 were collected from the intertidal portion of nearby Borodino Lake Creek, located about 7 km from LPW in the west end of the Port Walter Fiord. Borodino Lake Creek drains a lake that is inaccessible to migrating anadromous fish but has substantially higher stream discharge than Sashin Creek.

The highest straying frequency observed was 14.3% from 1986 brood Chickamin River subyearling releases (Table 3). However, returns were incomplete for this brood by 1989, and in this case, only seven adults were accounted for, including one recovered away from the release site. The highest straying frequency recorded for yearling smolt releases was 8.3% (60 total recoveries, incomplete returns) from 1986 brood Chickamin River fish. Other higher than average frequencies of strays recovered from releases of yearling smolts included 1987 brood Unuk River fish (5.7%, 335 recoveries, incomplete returns) and 1987 brood Chickamin

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Table 4. Summary of straying in LPW chinook salmon, 1981–1989, by population, sex, and coarse categories of adult age at recovery and run size.

Population	Sex	Adult age category (years)	Run size category	No. Homing	No. straying	% straying
Chickamin	F	<5	<1000	13	0	0.0
			≥1000	74	0	0.0
		≥5	<1000	2	9	81.8
			≥1000	456	3	0.6
Chickamin	M	<5	<1000	14	0	0.0
			≥1000	94	14	13.0
		≥5	<1000	2	3	60.0
			≥1000	835	3	0.4
Unuk	F	<5	<1000	181	1	0.6
			≥1000	2741	4	0.1
		≥5	<1000	315	8	2.5
			≥000	3448	49	1.4
Unuk	M	<5	<1000	247	12	4.6
			≥1000	5211	88	1.7
		≥5	<1000	436	5	1.5
			≥1000	6268	33	0.5

Note: Only sexed adults are included in this data set, which was extracted from the Pacific States Marine Fisheries Commission database.

River fish (6.7%, 135 recoveries, incomplete returns). However, recoveries from 1986 and 1987 brood releases included only age-2 (zero ocean winter) and age-3 (one ocean winter) fish in 1988 and 1989.

Males showed a greater tendency than females to stray; of 155 total strays recovered, 94 were male (1981–1987 recoveries; $G = 55.21$, 6 df, $P < 0.001$). Insufficient recoveries were made of Chickamin River fish to test directly for sexual differences in straying within this population; however, for the complete 1979–1983 broods of Unuk River fish, recoveries of stray fish varied significantly between the sexes ($G = 14.94$, 4 df, $P < 0.01$). A total of 94 males and 41 females were recovered as strays from these broods. The proportion of strays that were male varied from 38.5% (1979 brood Unuk River) to 85.7% (1980 brood Unuk River). Only in the 1979 brood were more female (16) than male (10) strays recovered. In all other broods, male recoveries exceeded female recoveries. We excluded age-2 (zero ocean winter) males, which may not travel far from LPW during the short period that they are at sea, from the analysis, but this did not change the conclusion that males strayed at higher rates ($G = 291.43$, 3 df, $P < 0.001$). The proportion of stray fish that were male did not vary significantly with run size ($F = 0.03$, 1 and 7 df, $P > 0.75$).

Based on recoveries of fish from five complete broods, regression of the proportion of fish straying on the number of winters spent at sea indicated that straying declined with increasing age in Unuk River fish ($r^2 = 0.97$, $P < 0.01$). Although straying was low at both ages at which most Chickamin River fish returned (ages 5 and 6), 6-year-old fish strayed at 1/10 the frequency of 5-year-olds (0.1 versus 1.3%). This difference was significant ($G = 6.69$, 1 df, $P < 0.01$) and could not be attributed to differences between males and females, as differences in overall sex ratios were small. In any case, this difference was opposite that expected if males had strayed at higher rates, with 59.5% male strays among 5-year-old fish and 71.9% male strays among 6-year-olds. The relationship between straying frequency and age was also significantly negative when the data from both populations were combined ($r^2 = 0.83$, $P < 0.01$) (Fig. 2*c*).

Evidence for a heritable straying component

Evidence that homing behavior may have a heritable component in some populations of chinook salmon (McIsaac and Quinn 1988; Pascual and Quinn 1994) led us to suspect that straying in LPW chinook salmon might differ between fish whose parents had experienced a spawning migration to LPW and those whose parents had not. Although these groups also differed in their environmental experiences, we compared broods that differed in this parental characteristic to test indirectly for a heritable straying component. Progeny of Unuk River parents whose gametes were transplanted directly to LPW (1976–1979 broods) strayed twice as often (1.9%) as those of parents who had returned to LPW after release (1982 and 1983 broods, 0.9%) ($G = 18.01$, 1 df, $P < 0.001$). Similarly, 1976 brood Chickamin River fish strayed more frequently (6.8%) than 1982 brood fish (1.3%) ($G = 12.14$, 1 df, $P < 0.001$).

To assess whether we could detect family differences in recovery patterns, we examined homing and straying recoveries of adults in full-sib families of Unuk River fish released from LPW as part of an independent experiment. A total of 170 578 yearling smolts were released in 36 full-sib families over two consecutive brood years (1984 and 1985). However, only three of the 915 adults (0.3%) recovered from these releases were strays, and each of the strays recovered was from a different family. No pattern could therefore be detected.

Multivariate analysis of factors affecting straying

We applied log-linear models to straying frequencies to evaluate effects of population, gender, run size, and adult age at recovery on straying. We first pooled data into two

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Table 5. Tests of alternative log-linear models for variation in straying.

Model	Interactions included	χ^2_F	df	*P*	χ^2_D	df	*P*	BIC
1	*PD + GD + AD + ND + PGD + PAD + PND + GAD + GND + AND + PGAD + PGND + PAND + GAND + PGAND*	0.46	1	>0.50	—	—	—	–9.5
2	*PD + GD + AD + ND + PAD + PND + GAD + GND + AND + PGAD + PGND + PAND + GAND + PGAND*	0.48	2	>0.75	0.02	1	>0.50	–19.4
3	*PD + GD + AD + ND + PAD + PND + GAD + GND + AND + PGND + PAND + GAND + PGAND*	1.25	4	>0.75	0.77	2	>0.50	–38.5
4	*PD + GD + AD + ND + PAD + GAD + GND + AND + PGND + PAND + GAND + PGAND*	9.17	7	0.25	7.92	3	>0.05	–60.3
5	*PD + GD + AD + ND + PAD + GAD + GND + AND + PAND + GAND + PGAND*	9.38	8	>0.25	0.21	1	>0.50	–70.1

Note: Factors considered here are the main effects of *P* (population), *G* (gender), *A* (adult age at recovery), *N* (number of fish in the escapement), and *D* (disposition: home or stray). Interactions are given as combinations of these effects; of interest here are the interactions between *D* and the other factors. The test statistic is the likelihood ratio χ^2. χ^2_F, test of the specified model's fit; χ^2_D, difference in χ^2 between the specified model and the previous (next less parsimonious) model. Raftery's Bayesian information criterion (BIC) decreases with increasing adequacy of the model to explain the pattern of variation. Model 1 is the saturated model; model 5 is the most parsimonious of the models that provides adequate fit to the data in Table 4. Interactions not shown in these models because they are trivial in the present context are *PG*, *PA*, *PN*, *GA*, *GN*, *AN*, *PGA*, *PGN*, *PAN*, *GAN*, and *PGAN*.

categories of run size and two of age at recovery to minimize the number of nonstructural zero cells in the data set. These pooled data are summarized in Table 4. We then fitted several hierarchical models to these data (Table 5). The most parsimonious model that provided the best explanatory power for these data, based on the likelihood ratio χ^2 and Raftery's BIC, was

$$(2)\quad \ln \hat{f}_{ijklm} = \mu + PD_{im} + GD_{jm} + AD_{km} + ND_{lm} + PAD_{ikm} + GAD_{jkm} + GND_{jlm} + AND_{klm} + PAND_{iklm} + GAND_{jklm} + PGAND_{ijklm}$$

This model, whose expression above includes only those terms involving interactions with straying disposition (*D*, homing or straying), confirmed the earlier analyses by indicating that population, gender, age at recovery, and run size all had significant effects on straying frequency. The power of log-linear modeling lies, however, in its ability to detect interactions among factors. Indeed, several first-order interactions with effects on straying were detected: those between population and age, gender and age, gender and run size, and age and run size. These interactions reflect several intriguing straying patterns (Table 4). First, the increased straying of younger fish was more evident in Chickamin River than in Unuk River fish. Second, straying tended to be higher in younger than in older males, but this pattern did not hold for females. Third, although straying was more frequent when runs were smaller, the pattern differed somewhat between males and females, with males tending to stray more when run size was small (however, the results were strongly skewed by two cells with small sample sizes). Finally, although straying tended to be higher at smaller run sizes, this pattern reflected greater straying in older Chickamin River fish but in younger Unuk River fish (however, small sample size again confounds this interpretation). The two second-order interactions indicate that the increase in straying at smaller run sizes varied by both population and gender. The single third-order interaction has no simple biological interpretation. Overall, the model in eq. 2 showed that straying patterns were correlated with the size and composition of the spawning run returning to LPW during the period of this study and that these features interacted to influence straying.

Discussion

Recoveries of adult LPW stream-type chinook salmon over 9 consecutive years indicate that straying of these fish was low. Despite a recent transplant history, some degree of isolation from final migration routes used by wild chinook salmon in southeastern Alaska, and the routine practice of releasing smolts directly into seawater without a downstream migratory experience, overall straying of LPW chinook salmon was only 1.2%. We conclude that newly transplanted hatchery fish do not necessarily stray at high rates. Our estimate is comparable with or lower than estimates published from studies that share similar limitations (discussed below) and indicates that strong imprinting to the release site did occur. Straying rates for hatchery chinook salmon in the Columbia River vary from <2 to >90% (Ellis and Noble 1960; Quinn and Fresh 1984; Quinn et al. 1991). Straying in ocean-type chinook salmon released from hatcheries in Oregon and California ranged from <1 to >40% (Sholes and Hallock 1979; Downey and Uremovich 1981, cited in Lister et al. 1981). Quinn et al. (1991), Pascual and Quinn (1994), and Pascual et al. (1995) concluded that straying patterns of Columbia River hatchery chinook salmon reflected a combination of race variation (stream versus ocean type), release location and timing, and environmental disturbance. Vander Haegen and Doty (1995) found that straying of Washington ocean-type chinook salmon was generally lower for coastal than for Columbia River stocks.

Sashin Creek, like nearly all other island streams in southeastern Alaska, does not support a natural chinook salmon run (Heard et al. 1995). The sources of chinook salmon nearest to LPW are hatcheries. One hundred and sixteen LPW chinook salmon were recovered at nine different hatcheries, including two facilities established from recent

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introductions at Hidden Falls and Port Armstrong on eastern Baranof Island (Fig. 1). In this study, these two hatcheries accounted for over one third of LPW fish recovered away from the release site. In particular, the operation of the Port Armstrong facility, a facility 11 km south of LPW that began culturing LPW-origin Unuk River stock in 1986, may have influenced recovery of 1986 and 1987 brood chinook salmon from LPW by attracting fish away from the release site.

Reliable estimation of salmon straying is difficult in the best of cases, and several problems are common to virtually all straying studies. In this study, we tried to avoid problems associated with marking effort and assumptions about behavior of unmarked fish (Quinn and Fresh 1984; Labelle 1992) by marking all fish. Although the definitive endpoint of homing or straying is reached when natural spawning occurs, homing and straying are typically estimated, as in this study, from recoveries of adult fish whether they have spawned or not. Unfortunately, any event that interrupts migration or spawning, such as capture at weirs, hatchery fences, or in terminal fisheries, precludes other prespawning options and may yield overestimates of straying rates (Ricker 1972; Quinn et al. 1991). On the other hand, failure to observe or recover fish will tend to underestimate true straying rates. The large number of southeastern Alaska streams to which chinook salmon might stray and spawn without detection suggests that inadequate and sporadic sampling could be an important source of error in our estimate of straying. Nevertheless, if straying from LPW was greatest to nearby streams, where our sampling effort was most extensive and most fish entering these streams were recovered, then our estimate of straying should not be much lower than the true frequency for chinook salmon released from LPW. The infrequent recoveries of LPW chinook salmon at more distant locations, even when hatchery recoveries were included, suggest to us that our overall estimate of straying in LPW chinook salmon is not likely to substantially underestimate the true frequency (e.g., by much more than a factor of 2).

No stream within a 150-km radius of LPW has a wild run of chinook salmon, with the possible exception of the Redoubt Lake outlet stream on the west coast of Baranof Island (85 km distant; Fig. 1) where unmarked adult chinook salmon have been observed occasionally (A. Schmidt and D. Barto, Alaska Department of Fish and Game, Sitka, Alaska, personal communication, May 1986). From 1983 to 1989, six LPW fish were recovered in the Farragut River, the system closest to LPW known to support an endemic population of chinook salmon (Heard et al. 1995). Other LPW chinook salmon recovered in wild chinook salmon systems included two in the Taku River and one in the Stikine River, both large mainland systems (Fig. 1). We were unable to verify anecdotal evidence for three additional recoveries of LPW fish in the Stikine River between 1988 and 1989.

The spatial pattern of straying of LPW chinook salmon shows a northern bias that could help identify predominant routes used by adults on the final phase of their return migration. Stream-type chinook salmon from southeastern Alaska are thought to migrate farther west in the Gulf of Alaska than ocean-type chinook salmon, but these fish evidently use the inside waters of southeastern Alaska as a nursery for an extended period and may have restricted marine migrations (Healey 1991). Patterns of marine recoveries of coded-wire-tagged LPW chinook salmon in southeastern Alaska imply that some fish enter the southern end of Chatham Strait as they return (Fig. 3), but we could not determine whether this was their primary migratory route. Recoveries of coded-wire-tagged LPW fish in the southeastern Alaska commercial fishery indicate that most (84.2%) of the 8632 LPW fish recovered in this fishery between 1981 and 1989 were caught in Alaska Department of Fish and Game fishing districts 109, 110, and 112 (Fig. 3) and that 79.4% of the LPW fish recovered were caught between June and August. More fish were caught in district 109 in June but in districts 110 and 112 in July and August (χ^2 = 2043.61, 42 df, $P < 0.0001$); within district 109, 75.1% of the 3039 fish caught in the southern part of the district in summer were recovered in June and July, but only 45.5% of the 145 fish caught in the northern part of the district in summer were recovered then. Most (82.5%) of the 57 fish caught in district 104 were caught in July and August; just over half (58.1%) of the 434 fish caught in district 113 were also recovered in these months. Collectively, these patterns imply not a single migratory pathway for maturing fish returning to LPW, but instead multiple routes through Chatham Strait, Icy Strait, and possibly Frederick Sound.

Adult chinook salmon returning to LPW are recovered at the Sashin Creek weir; they are not permitted to spawn there. However, collection is imperfect, and the environmental conditions that usually exist at LPW during late summer may induce wandering behavior and, ultimately, straying because flow and temperature conditions do not meet the environmental requirements of Alaskan chinook salmon for spawning and incubation (Healey 1991), at least in some years. When adult chinook salmon are returning to the LPW estuary, the creek typically has low discharge (≤ 0.5 $m^3 \cdot s^{-1}$) and warm temperatures (15–20°C), unlike typical mainland chinook salmon streams in southeastern Alaska that are large, fast flowing (>10 $m^3 \cdot s^{-1}$), and cool (8–12°C) during the adult return. This contrast was especially evident in 1981, when unusually low stream discharge from Sashin Creek led to movement of many of them into other Port Walter Fiord streams.

Two observations support the hypothesis that straying in chinook salmon has a heritable component: (*i*) straying was higher in Chickamin River than in Unuk River fish over the same period and under similar culture conditions and (*ii*) straying was higher in offspring of adults that had homed to the ancestral river than in first-generation offspring of transplanted adults that had returned to LPW. The possibility that this component may reflect a maternal or common environmental element cannot be excluded, however. The component could be a residual effect of the transplant (e.g., assimilation of a biochemical agent during incubation that interfered with subsequent imprinting). Such an effect should diminish markedly within one generation of the transplant, and our observations are consistent with this hypothesis.

Apparently more important to straying than the effect of any heritable component, however, were the influences of proximate environmental factors during the adult migration. Small sample sizes limited our confidence in inferring some

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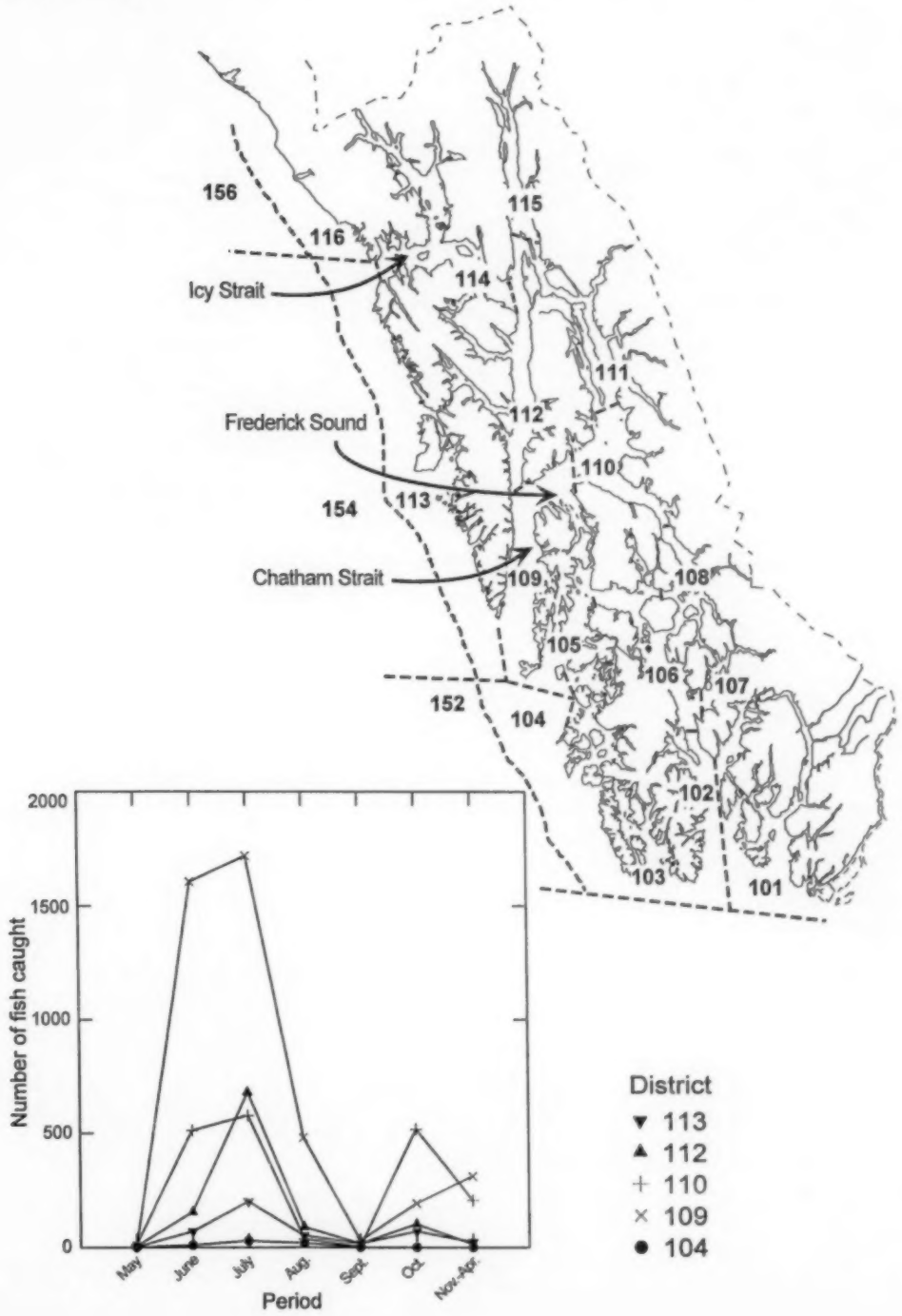
Fig. 3. Spatial and temporal patterns of harvest of coded-wire-tagged LPW chinook salmon in selected southeastern Alaska fishery districts. Districts represent several near the LPW terminal area. Data are summarized from the Pacific States Marine Fisheries Commission database. Chatham Strait, Icy Strait, and Frederick Sound indicate possible migration routes for chinook salmon returning to LPW. See text for discussion.



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contrasts, but these influences appeared to be complex (Table 4). Straying was more frequent among younger fish, but the trend was greater in Chickamin River fish (where young fish were fewer) than in Unuk River fish. Straying in males was largely responsible for the inverse relationship between straying and age. In small runs, straying was also higher in males than in females, especially for Unuk River fish. The combination of these interactions with our inability to detect appreciable culture influences leads us to reject our null hypothesis and conclude that run composition and environmental conditions experienced during the final phase of the spawning migration had substantial effects on straying.

That males strayed more than females is largely responsible for the observation that older fish strayed less than younger fish. This pattern contrasts with the conclusions of other investigators (Quinn and Fresh 1984; Quinn et al. 1991; Unwin and Quinn 1993) who found greater straying in older fish. The reason for this discrepancy may stem from the greater range of maturation ages in Alaskan chinook salmon, differences in sex ratio, or environmental differences experienced by migrating salmon near the imprinting site. The correspondence between low straying and complex age structure in LPW chinook salmon is consistent with Quinn's (1984) hypothesis for an inverse relationship between spatial and temporal risk-spreading as mechanisms to avoid catastrophic events in the home stream. In any case, our data do not support the notion that memory loss is an important problem for homing (Quinn and Fresh 1984; Quinn et al. 1991).

Why should males stray more frequently than females? We believe that this pattern reflects sex-specific reproductive tactics. Female Pacific salmon increase their fitness by maximizing body size (thereby increasing fecundity and ability to establish breeding territories), minimizing prereproductive mortality, and acquiring and defending nesting sites (Foote 1990; Fleming and Gross 1994). Males compete with each other for access to females and breeding sites, and reproductive success is determined by the number of offspring sired. This success is largely a function of mating opportunities, which can be heavily influenced by male size through both intermale competition and female mate choice (Hanson and Smith 1967; Schroder 1982; Foote 1989; Quinn and Foote 1994). Male Pacific salmon show a greater readiness for reproduction and greater variance in reproductive success than females (Fleming and Gross 1994); greater male promiscuity might under some circumstances encourage straying to increase the probability of avoiding contest or finding uncontested females. Straying may also permit males to circumvent the disadvantages of small male body size in mate competition (Hanson and Smith 1967; Quinn and Foote 1994), particularly when the operational sex ratio is highly biased toward males. The slope of a regression of sex ratio in straying LPW fish on sex ratio in the terminal run ($b \pm 2$ SE = 1.03 ± 0.82) did not differ from 1.0, suggesting that male straying was not frequency dependent, at least at that stage of the run.

Although straying LPW fish represented only a small fraction of all mature adults recovered during this study, straying to areas where wild populations occur poses genetic and ecological threats to these populations. To a first approximation, the proportion of straying fish in the recipient population — not the straying frequency in the donor population — determines the magnitude of these threats (Grant 1997). The significance of finding nine LPW fish in three wild chinook salmon systems during this study, apart from documenting that this straying occurred, is not clear. Based on the almost complete restriction of wild chinook salmon in southeastern Alaska to large and often glacially influenced mainland rivers, the reproductive success of straying hatchery fish in these systems may be low. Nevertheless, some streams, such as the Farragut River, appear to be attractive to wandering chinook salmon (Heard 1996), a situation that increases the possibility for gene flow from hatchery to natural populations. Our findings indicate that factors that have substantial effects on straying of hatchery fish may be only partially under hatchery control, and these effects could offset increases in homing that result from improved culture practices. Future monitoring of straying patterns in southeastern Alaska hatchery chinook salmon is necessary to document interactions with wild populations and to identify aquacultural practices that reduce risks to natural salmon populations posed by straying hatchery fish.

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Trophic position and individual feeding histories of fish from Lake Okeechobee, Florida

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Abstract: We used C and N stable isotope measurements to identify trophic position and feeding histories of fish from Lake Okeechobee, one of the largest lakes in North America. When $\delta^{15}N$ values were used to estimate trophic levels, analyses of about 500 individual fish collected in two seasons at five sites showed that trophic level varied from 2 (herbivore) to 4.3 (second-level carnivore) among the 29 fish species examined. Lower trophic levels predominated among small fish caught at a littoral marsh site, and highest trophic levels were found among larger offshore fish. Marsh fish showed about three times the C isotope variation than did offshore fish, consistent with the wider array of foods in the marsh versus offshore food web. In addition to these community-level results, there were often unexpected large isotopic differences between individuals in almost all fish species examined, suggesting large differences in individual feeding behavior. Isotopic analyses indicate long-term differences in feeding among individuals, in addition to the short-term differences often observed in stomach content studies. Long-term individual variation in fish foraging may be important in understanding variation in other biochemical parameters measured in fish, such as Hg or PCB contents.

Résumé : Nous avons procédé à des mesures à l'aide d'isotopes stable du C et de le N afin de déterminer la position trophique et le comportement alimentaire des poissons du lac Okeechobee, un des plus grands lacs d'Amérique du Nord. Des analyses fondées sur les valeurs de $\delta^{15}N$ nous ont permis de classer en fonction de leur niveau trophique les quelque 500 poissons récoltés pendant les deux saisons de l'étude dans cinq sites différents. Ces analyses ont révélé que les 29 espèces examinées étaient réparties entre les niveaux trophiques 2 (herbivore) et 4,3 (carnivore de deuxième niveau). La plupart des poissons de petite taille capturés dans un marais côtier appartenaient à un faible niveau trophique, tandis que les poissons de plus grande taille capturés à une certaine distance des rives appartenaient en général à un niveau trophique plus élevé. La variabilité des mesures à l'aide d'isotopes du C chez les poissons du marais était environ trois fois supérieure à celle observée chez les poissons du large. Ces différences s'expliquent par la plus grande diversité de nourriture dans le marais que dans la chaîne trophique du large. Outre ces résultats intéressant des communautés entières, nous avons observé des écarts à la fois importants et souvent inattendus dans les lectures isotopiques entre presque tous les poissons examinés. Ces différences individuelles semblaient liées à des différences de comportement alimentaire. Les analyses isotopiques ont également fait ressortir des différences à long terme de comportement alimentaire entre les individus, en plus des différences ponctuelles souvent révélées par analyse des contenus stomacaux. La variation individuelle à long terme du comportement de quête de nourriture pourrait jouer un rôle déterminant dans la variation d'autres paramètres biochimiques mesurés chez les poissons comme les concentrations de Hg ou de PCB.

[Traduit par la Rédaction]

Introduction

Although animals spend much of their time feeding, and foraging success is essential for reproductive success and fitness, it is often difficult to quantify foraging in free-living aquatic organisms. Stable isotopes can be used as natural tracers to help monitor fish foraging histories.

The natural stable isotopic compositions of animals are determined by their diets. Isotopic variations arise at the plant and bacterial level during uptake of nutrients and CO_2 (Fry and Sherr 1984; Peterson and Fry 1987) and are passed up the food web as animals accumulate tissue C and N from their diets. Most stable isotopic studies focus on determining which sources of plant nutrition are most important in sup-

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porting animal consumers in food webs (e.g., Fry and Parker 1979; France 1994), but the natural isotopic tracers also can be used in a different manner, to monitor animal behavior. For example, animals feeding in some locations acquire a unique biogeochemical composition that functions as a natural tag if they migrate into a second area where foods with a different average isotopic composition are eaten and assimilated. Aquatic-feeding animals as diverse as shrimp, whales, and ducks have been studied with stable isotopes to address movements and migrations, rather than diets per se (Fry 1981; Schell et al. 1989; Trust 1993).

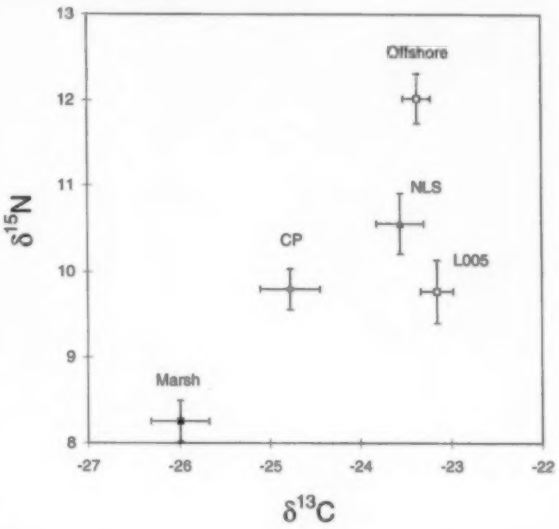
Because C and N isotopes are accumulated in tissues over substantial periods of time, the isotopes are time-integrated measures of diet and foraging (Gannes et al. 1997). The length of the dietary time integration varies with the tissue and size of the animal, but for muscle tissue of adult fish, the time integration is 1 year or greater (Hesslein et al. 1991, 1993). Given this lengthy period, it is reasonable to expect that for many mobile fish species, even in large lakes, individuals should have similar isotopic compositions if they have similar long-term average diets. An alternative hypothesis is that individual fish are much more specialized than we commonly perceive, focusing on specific diets or remaining in restricted habitats, and this specialization leads to large between-individual dietary and isotopic differences within single species. We tested these alternatives in the fish community (common and scientific names of fish species studied are given in the caption to Fig. 2) of a large lake, Lake Okeechobee of south-central Florida, U.S.A., using a combination of N and C stable isotopes to assess long-term individual diets.

Methods

Fish were collected using several techniques, including otter trawls, electrofishing, rotenone in combination with electroshocking, and haul seining conducted by commercial fishers. Details of fish collection methods are given elsewhere (Furse and Fox 1994; Bull et al. 1995). Specimens were collected in late August 1996 and mid-January 1997 from five sites in Lake Okeechobee: a marsh site (Moore Haven (MH) 24 000, 81°01′11″W, 26°52′37″N, near the center of the large littoral marsh on the western side of the lake), three nearshore sites (Cochran's Pass (CP), 80°57′55″W, 26°53′27″N, at the boundary between marsh and open water, L005, 80°58′20″W, 26°57′23″N, an open-water site within 1 km of marsh habitats, and North Lake Shoal (NLS), 80°49′54″N, 27°04′58″W, an open-water site also within 1 km of marsh habitats), and an offshore site (LZ40, 80°47′18″W, 27°54′08″N, in the central open-water area of the lake). The sites were chosen to represent major habitat areas within the lake (Aumen and Wetzel 1995).

Fish were transported on ice to the laboratory of the Florida Game and Fresh Water Fish Commission in Okeechobee, Fla. In the laboratory, fish were identified to species, weighed wet to the nearest 0.01 g, and total length, standard length, and fork length (where possible) recorded for each specimen. White muscle tissue was dissected from the middorsal region of each fish, dried at 60°C, and then crushed to a fine powder for isotopic determination. Tissue samples (0.4–0.8 mg) were analyzed with a continuous-flow analysis system consisting of a Carlo Erba elemental analyzer interfaced to a Finnigan Delta C mass spectrometer. Results are reported as parts per thousand (‰) deviations from internationally recognized reference materials, PDB ($\delta^{13}C$) and N_2 in air ($\delta^{15}N$). Replicate analyses of the same powdered sample usually agreed within 0.2‰ or better. Samples enriched in ^{13}C or ^{15}N are relatively "heavy" and have higher δ values, while samples depleted in ^{13}C or ^{15}N are "lighter" and have lower δ values.

Fig. 1. Overall $\delta^{13}C$ and $\delta^{15}N$ averages (± 95% confidence limits) for fish sampled at the five study sites. Sampling sites included a marsh site (Moore Haven 24 000), three nearshore sites (Cochran's Pass (CP), L005, and North Lake Shoal (NLS)), and an offshore midlake site (LZ40).



Results

On a broad community level, fish taken at the marsh site had the lowest C and N isotopic compositions, offshore specimens had the highest values, and fish taken at three nearshore sites had intermediate values (Fig. 1; Appendix Tables A1 and A2). The lowest $\delta^{15}N$ values for a single species averaged 5.6‰ and occurred in sailfin molly from the marsh habitat (Fig. 2). The highest average values were 13.6‰ and occurred in Florida gar collected offshore (Fig. 2). Given the assumption of 3.4‰ ^{15}N increase per trophic level (Minagawa and Wada 1984), this 8‰ ^{15}N increase across the fish community denotes about 2.3 trophic levels (Fig. 2).

Isotopic compositions of fish showed little seasonal difference between August and January specimens (Appendix Tables A1 and A2). There was usually no systematic variation with size (Figs. 3–7), with the notable exceptions that $\delta^{15}N$ values increased with size for bowfin, largemouth bass, and Florida gar (Fig. 6). While seasonal and most size-related isotopic changes were small, strong isotopic differences were associated with the site of collection along a marsh–offshore gradient (Fig. 1). There was a transition from low to high $\delta^{13}C$ and $\delta^{15}N$ values occurring in species that are found in shallow-water marshes when young, but often move offshore as larger adults (e.g., largemouth bass and Florida gar, Fig. 6). Some species such as the black crappie and various catfish (Figs. 3 and 4), which are usually caught offshore (Miller et al. 1990; Bull et al. 1995), had fairly constant C isotopic compositions consistent with limited use of nearshore marshes. Nearly constant and similar $\delta^{13}C$ values among these species indicate that a well-mixed organic mat-

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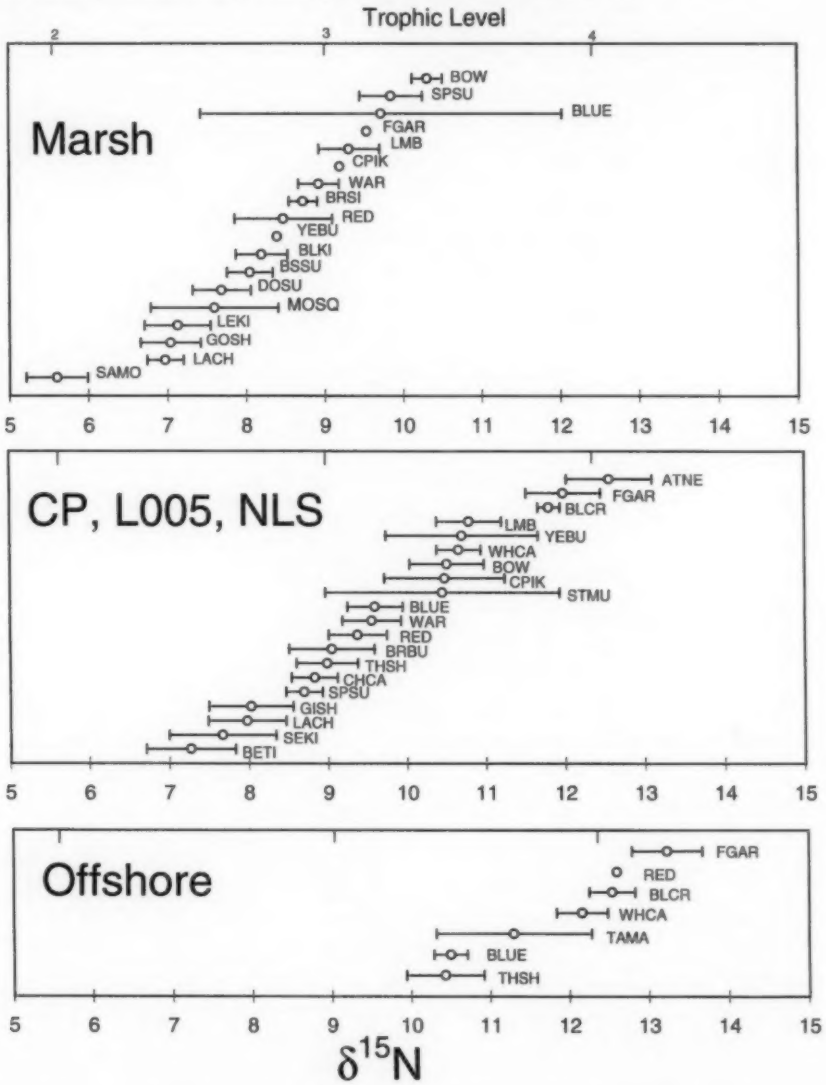
Fig. 2. Mean $\delta^{15}N$ values (±95% CL) and estimates of fish trophic levels at the five sites; data combined from all collections. ATNE, Atlantic needlefish (*Strongylura marina*); BETI, blue tilapia (*Tilapia aurea*); BLCR, black crappie (*Pomoxis nigromaculatus*); BLKI, bluefin killifish (*Lucania goodei*); BLUE, bluegill (*Lepomis macrochirus*); BOW, bowfin (*Amia calva*); BRBU, brown bullhead (*Ameiurus nebulosus*); BRSI, brook silverside (*Labidesthes sicculus*); BSSU, bluespotted sunfish (*Enneacanthus gloriosus*); CHCA, channel catfish (*Ictalurus punctatus*); CPIK, chain pickerel (*Esox niger*); DOSU, dollar sunfish (*Lepomis marginatus*); FGAR, florida gar (*Lepisosteus platyrhincus*); GISH, gizzard shad (*Dorosoma cepedianum*); GOSH, golden shiner (*Notemigonus crysoleucas*); LACH, lake chubsucker (*Erimyzon sucetta*); LEKI, least killifish (*Heterandria formosa*); LMB, largemouth bass (*Micropterus salmoides*); MOSQ, eastern mosquitofish (*Gambusia holbrooki*); RED, redear sunfish (*Lepomis microlophus*); SAMO, sailfin molly (*Poecilia latipinna*); SEKI, Seminole killifish (*Fundulus seminolis*); SPSU, spotted sunfish (*Lepomis punctatus*); STMU, striped mullet (*Mugil cephalus*); TAMA, tadpole madtom (*Noturus gyrinus*); THSH, threadfin shad (*Dorosoma petenense*); WAR, warmouth (*Lepomis gulosus*); WHCA, white catfish (*Ameiurus catus*); YEBU, yellow bullhead (*Ameiurus natalis*).



ter source, probably offshore phytoplankton, fuels the food web leading to these fish.

We used our field data to estimate isotopic similarity expected for fish feeding on a single or uniform diet. Previous laboratory studies for animals raised on controlled diets show between-individual $\delta^{13}C$ and $\delta^{15}N$ variation (ranges) of <2‰ (DeNiro and Epstein 1978, 1981), while field collections of fish from the offshore Gulf of Mexico show similar small $\delta^{13}C$ ranges of 0.7–1.4‰ when n = 41–54 fish (Fry and Parker 1979). In this field study of Lake Okeechobee, a 1.5‰ range among individuals for both C and N isotopes was found for 25 black crappie of various sizes collected in

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Fig. 3. Isotope changes by size for black crappie and $\delta^{15}N$ and $\delta^{13}C$ summary plots. Left panels, all data; middle panels, collections made in August 1996 (solid symbols represent values for fish collected at offshore station LZ40); right panels, data from three of four stations in the January 1997 collections.

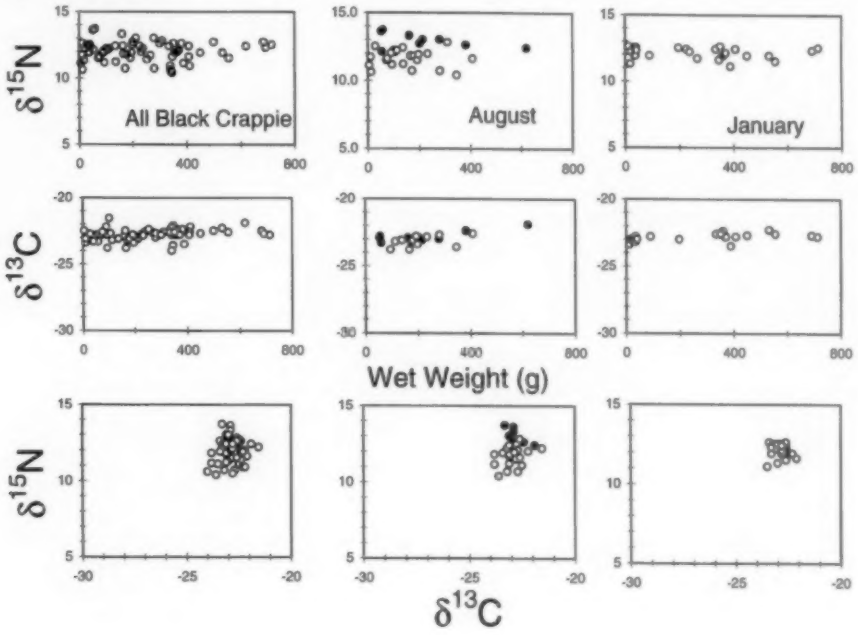

Fig. 4. Isotope changes by size for different catfish species and $\delta^{15}N$ and $\delta^{13}C$ summary plots. For channel catfish, open symbols represent fish collected at L005 and solid symbols represent fish collected at NLS. For bullhead catfish, solid symbols represent yellow bullhead and open symbols represent brown bullhead.

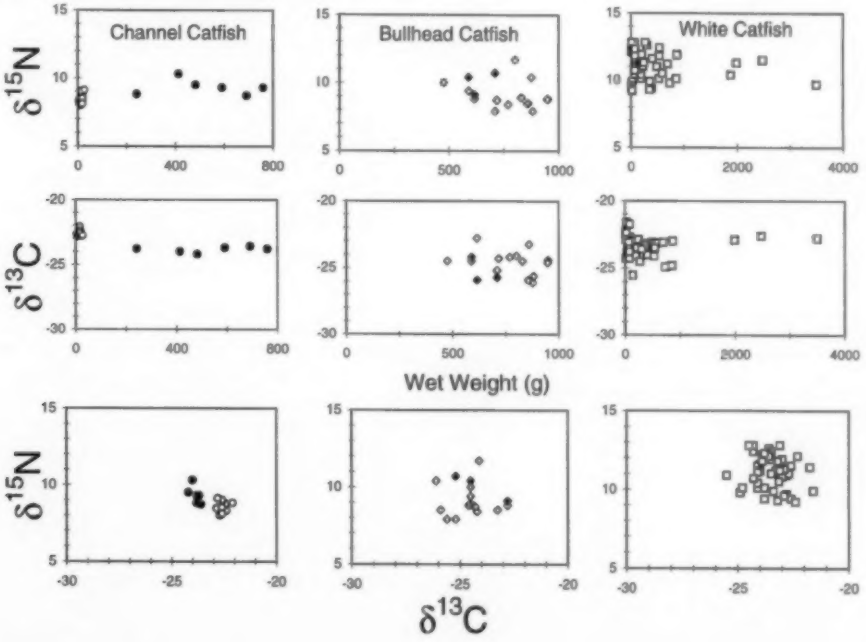

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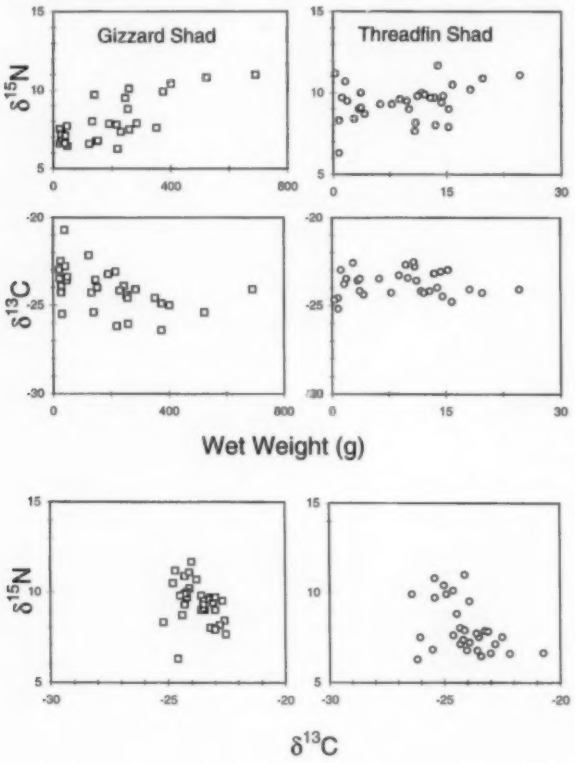
Fig. 5. Isotope changes by size for gizzard shad and threadfin shad and $\delta^{15}N$ and $\delta^{13}C$ summary plots; data combined for all sites and seasons.



January 1997 at three stations (Fig. 3, right panels), and narrow isotope ranges occurred for two separate August collections of channel catfish collected from L005 and NLS (Fig. 4, left panels). Overall, narrow isotopic ranges of 0.8–1.3‰ occurred for both $\delta^{13}C$ and $\delta^{15}N$ in five of 32 cases examined where eight or more fish were collected together. These narrow ranges (1–1.5‰) among individuals encompass sampling and analysis errors and provide a rather strict standard for judging dietary similarity among individuals. Fish whose isotopic compositions differed by amounts greater than these limits presumably had fed on different diets. Using these criteria, dietary differentiation between individual fish was common in most species and applied even for larger sized fish where long-term feeding might have been expected to average out individual feeding differences. The largest isotopic differences among individuals collected together occurred for several small-bodied fish from the marsh site (Fig. 8).

Discussion

Trophic levels among fish species of Lake Okeechobee ranged from herbivore (trophic level 2, e.g., sailfin molly) to carnivores (trophic level 3, e.g., bowfin) to piscivores (trophic level 4–4.3, e.g., large Florida gar) (Fig. 2). The lowest trophic levels ($\delta^{15}N$ values) were found among the smallest marsh fish and the highest trophic levels were found in large fish collected offshore (Fig. 2). Similar numbers of trophic levels have been found in many other aquatic studies in which $\delta^{15}N$ was used as the trophic level indicator (Minagawa and Wada 1984; Fry 1988; Gu et al. 1996; Keough et al. 1996; Zanden et al. 1997) but are less than those predicted in studies of potential food web complexity (up to six to nine trophic levels, Sprules and Bowerman 1988; Schoener 1989). While it is possible that the $\delta^{15}N$ metric underestimates the importance of linkages in the microbial loop (Meili et al. 1993; Fry and Quinones 1994), thus reducing the apparent food web length by one or two trophic levels, omnivory and opportunistic feeding are likely responsible for the more compact food webs realized in nature (Kling et al. 1992; Havens et al. 1996).

Fish collected in this study showed a wide range of 11.5‰ in C isotopic compositions (Appendix Table A1) that is much broader than the 3–5‰ range observed in most offshore marine studies (Fry and Sherr 1984). The wider isotopic range is due to the presence of a large marsh that comprises some 20% (52 600 ha) of the surface area of Lake Okeechobee. In this lake, fish that spent most of their lives offshore showed a much narrower 2–4‰ range similar to that observed in marine systems, while collections at sites associated with the littoral marsh extended the $\delta^{13}C$ range both well above and well below the offshore range. This larger $\delta^{13}C$ range in marsh fish from Lake Okeechobee must be underlain by a large $\delta^{13}C$ diversity in marsh foods that could include macrophyte detritus, phytoplankton, and various kinds of attached algae. Marsh habitats in Lake Okeechobee are extensive and quite heterogeneous in both time and space (Aumen and Wetzel 1995), and the inferred $\delta^{13}C$ diversity for marsh foods is similar to that documented in other studies of plant and prey isotopic compositions in freshwater marshes (Boon and Bunn 1994; Keough et al. 1996). Relatively high ^{13}C-enriched values have been reported for fish collected from some littoral freshwater habitats versus values for fish collected offshore (Hecky and Hesslein 1995), but this was not observed in the Lake Okeechobee marsh collections. The relatively low $\delta^{13}C$ values of marsh fish versus offshore fish in this lake may indicate larger inputs of –27‰ C_3 macrophyte detritus in the marsh food web or use of ^{13}C-depleted respired CO_2 by marsh microalgae (Keough et al. 1996).

Most offshore-feeding fish had similar, constant $\delta^{13}C$ isotopic compositions in the –22 to –24‰ range that were significantly higher than values found in marsh-feeding fish (Figs. 1, 3, and 4). Fish that move offshore from marshes should change from low marsh values towards these offshore values, and this was observed for bowfin, largemouth bass, Florida gar, and redear sunfish (Figs. 6 and 7). Addition of new C from the offshore food web, as well as turnover and loss of the old marsh C, leads to asymptotic changes in isotopic values with size (Fry and Arnold 1982) that were generally observed for these species. Increases in $\delta^{15}N$ with size for the fish of Fig. 6 indicate increasing trophic level, consistent with increased piscivory at larger sizes (Gu et al. 1996).

However, some individuals deviate strongly from the overall trend for the species (e.g., the largest individual largemouth bass and next-to-largest individual bowfin, Fig. 6). These individual "isotope eccentrics" had isotopic compositions consistent with prolonged use of marsh habitats, rather

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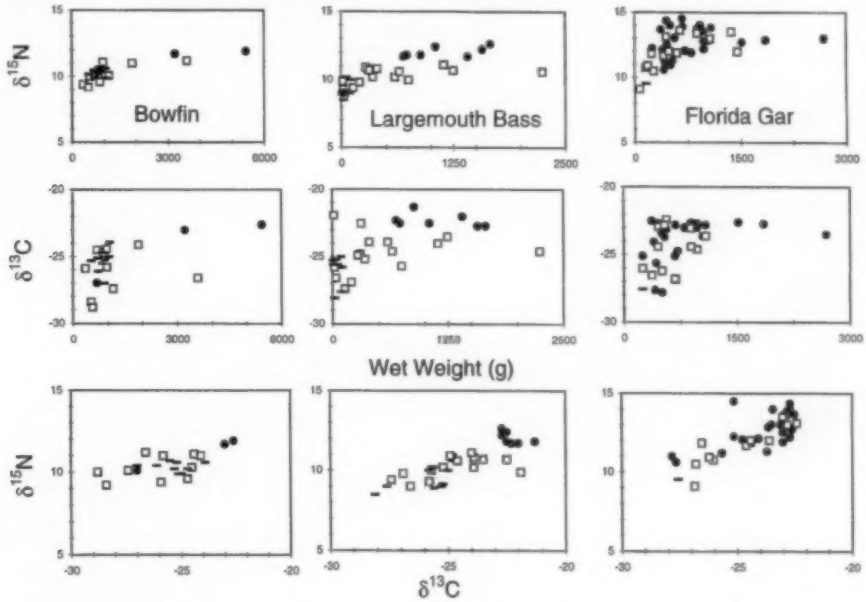
Fig. 6. Isotope changes by size for bowfin, largemouth bass, and Florida gar and $\delta^{15}N$ and $\delta^{13}C$ summary plots. Collection site: dashes, MH marsh; open squares, CP; solid circles, other sites (L005, NLS, LZ40).



than long-term residency offshore (i.e., their values are more similar to those of marsh fish versus offshore fish of Fig. 1). Isotope diversity among individuals also was strong at the CP station for species such as redear sunfish and bluegill (Fig. 7). The diversity may indicate that individuals caught at CP specialize on diverse foods available at this ecotonal interface station. Behavioral studies have shown that individual bluegill may specialize in their feeding behavior (Ehlinger and Wilson 1988). Individual redear sunfish and bluegill collected at the other two nearshore stations (L005 and NLS) located further offshore in open water showed much less isotope diversity and –22 to –24‰ values (Fig. 7), suggesting longer-term residency offshore.

For fish species that live continuously in either offshore or marsh habitats, the causes of between-individual differences in isotopic compositions are less clear. For example, August collections of channel catfish at NLS and L005 yielded two groups with disjunct isotopic compositions (Fig. 4), with both groups having C isotopic compositions in the –22 to –24‰ $\delta^{13}C$ range associated with offshore feeding. One explanation is that the two groups of animals were traveling in separate schools and were using different feeding grounds near the marsh – open water interface. We do not know if these feeding grounds yield prey organisms with different isotopic compositions, leading to the isotopic differentiation in fish predators. This seems possible, given known differences in invertebrate communities across the lake (Warren et al. 1995), but will require further sampling of organisms less mobile than fish to establish the geographic isotope pattern in offshore feeding grounds.

A second noteworthy example of between-individual isotope variation among offshore-dwelling organisms concerns August collections of intermediate-sized black crappie and Florida gar at offshore station LZ40. $\delta^{15}N$ values of these animals were the highest of any fish sampled (Fig. 3, top and bottom middle panels; highest values in top right panel of Fig. 6) and would normally denote animals occupying the highest trophic level in the lake. An alternative explanation is that these fish had recently consumed foods with high $\delta^{15}N$ and that this effect was strongest in smaller fish where newly acquired prey N would be less diluted by preexisting tissue N than in larger fish. Analyses of prey $\delta^{15}N$ are needed to check this alternative explanation of highest $\delta^{15}N$ in relatively small fish. Changing diet coupled with different dynamics of tissue turnover is thus one possible source of between-individual isotopic variation. Variable lipid compositions can also affect muscle $\delta^{13}C$ values in lipid-rich fish species such as shad (Gu et al. 1996).

It was surprising that the largest offshore fish did not always have very similar isotopic compositions, as might be expected from long-term diet averaging. Tight isotope clustering was not observed for large white and brown bullhead catfish (Fig. 4), for large blue tilapia in another Florida lake (Gu et al. 1997), and for larger offshore marine fish (Wainright et al. 1993). These results suggest long-term, individual-level variation in diet that may be important in explaining individual-level variability in other biochemical characteristics, such as Hg or PCB contents. Integrating isotope studies in limnological surveys (e.g., Bachmann et al. 1996) may help explain variation in these contaminants and generally provide a relatively inexpensive way to monitor long-term changes in fish trophodynamics within and across lakes.

Collections from the marsh site showed the largest between-individual isotopic variation, in this case applying to small-bodied fish with limited dispersion capabilities. Brook silverside showed the least between-individual isotopic variation (Fig. 8), which may be due to feeding on a relatively well-mixed planktonic food resource. The remaining fish of

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Fig. 7. Isotope changes by size for redear sunfish and bluegill and $\delta^{15}N$ and $\delta^{13}C$ summary plots. Collection site: dashes, MH marsh; open squares, CP; solid circles, other sites (L005, NLS, LZ40).

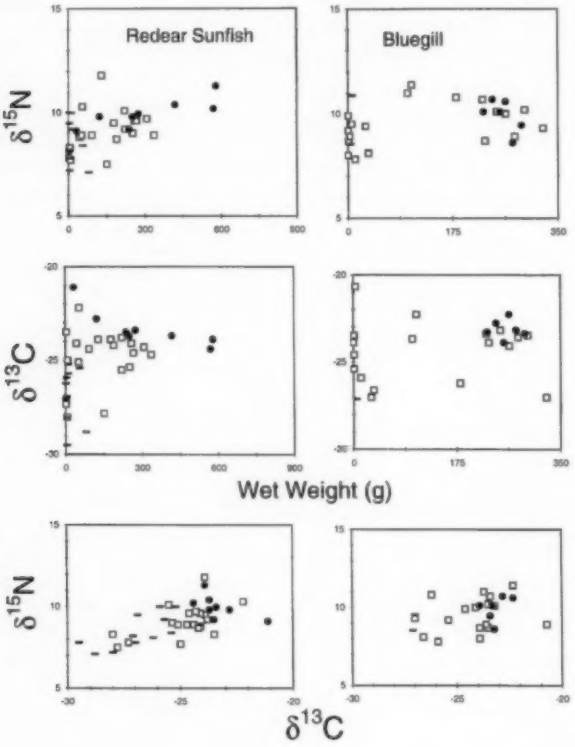

Fig. 8. Within-species isotopic ranges (polygons) among individual small fish (<10 cm total length) at the marsh site, August 1996. Squares, redear sunfish; circles, brook silverside; triangles, golden shiners; diamonds, least killifish.

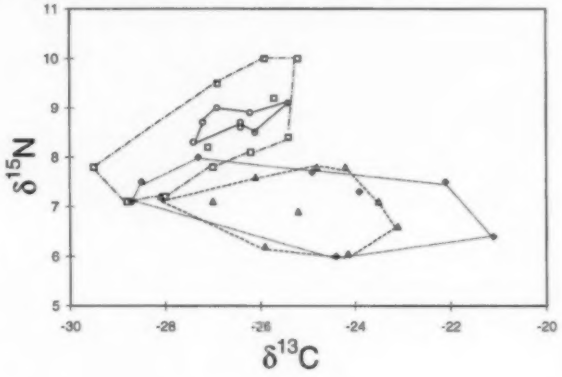

Fig. 8 are more benthic in their feeding and, in order to have the very strong isotopic differences observed between individuals, must encounter an isotopically diverse prey base and also specialize in some manner during feeding. The nature of this specialization still needs to be established and may be different for different species. For example, individuals of some species might localize feeding in a small home area that limits access to a broader diet, while in other species, individuals might range more widely but truly specialize on certain prey items that they select. This latter type of specialization was detected in earlier stable isotope studies of terrestrial herbivores where individual grasshoppers ate different mixtures of C_3 and C_4 plants (Fry et al. 1978).

Overall, this study shows that isotopic analyses are sensitive indicators of between-individual differences in diet. Because individual variation can be the basis for selection leading to evolution of new behaviors, further studies seem warranted using these and other biogeochemical markers (e.g., Hg, Cs, organic contaminants, Kiriluk et al. 1995) of fish movement and behavior. These chemical tracer analyses provide a long-term overview of differences in individual feeding histories, complementing shorter-term observational and behavioral studies. More detailed biogeochemical feeding histories may be available ultimately via sequential analyses of organic materials laid down in fish scales; such a chronological approach with baleen has proved valuable for following diets and migrations of free-living whales (Schell et al. 1989).

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Table A1. Fish $\delta^{13}C$ ± 95% confidence level (n = number of individuals) for August 1996 and January 1997 by site.

		Cochran's Pass		L005		North Lake Shoal		LZ40	
Species	Moore Haven, August	August	January	August	January	August	January	August	January
Florida gar	–29.57 (n = 1)	–25.81±0.92 (n = 4)	–24.04±1.01 (n = 10)	–24.87±1.56 (n = 2)		–25.32±2.04 (n = 5)	–23.05±0.88 (n = 8)	–23.39±0.67 (n = 9)	–22.94±0.23 (n = 8)
Bowfin	–25.31±0.57 (n = 6)		–26.06±1.05 (n = 10)				–24.20±2.75 (n = 3)		
Gizzard shad		–24.28±0.32 (n = 2)	–24.10±0.69 (n = 4)		–23.73±0.54 (n = 10)	–23.89±1.05 (n = 10)	–25.43±0.67 (n = 4)		
Threadfin shad		–24.13±1.54 (n = 3)		–23.09±0.21 (n = 10)	–23.96±0.33 (n = 10)				–24.04±0.31 (n = 10)
Golden shiner	–25.21±0.98 (n = 10)								
Lake chubsucker	–26.61±0.57 (n = 10)		–27.67±0.84 (n = 10)						
White catfish		–23.45±0.75 (n = 10)		–22.92±0.24 (n = 10)	–23.40 (n = 1)	–23.51±0.33 (n = 7)	–23.60±1.01 (n = 6)	–23.36±0.21 (n = 5)	–24.02±0.22 (n = 10)
Brown bullhead		–24.09±0.60 (n = 7)	–25.33±0.83 (n = 3)	–24.50 (n = 1)			–24.93±1.18 (n = 3)		
Yellow bullhead	–25.40 (n = 1)	–24.20 (n = 1)	–25.27±0.20 (n = 2)						
Channel catfish				–22.58±0.14 (n = 10)		–23.85±0.17 (n = 6)			
Tadpole madtom									–23.80±0.20 (n = 2)
Chain pickerel	–26.30 (n = 1)		–24.90 (n = 1)				–23.70±1.88 (n = 3)		
Atlantic needlefish					–22.10 (n = 1)		–22.48±0.17 (n = 4)		
Seminole killifish			–24.96±0.41 (n = 5)						
Brook silverside	–26.50±0.45 (n = 8)								
Warmouth	–26.00±0.71 (n = 3)		–27.19±1.13 (n = 10)						
Bluegill	–22.60±8.82 (n = 2)	–23.76±0.69 (n = 10)	–24.46±1.55 (n = 10)			–23.12±0.53 (n = 5)	–23.20±0.21 (n = 4)		–23.16±0.23 (n = 10)
Redear sunfish	–26.88±0.83 (n = 11)	–23.81±0.84 (n = 10)	–25.46±1.00 (n = 10)	–22.90±0.93 (n = 5)			–24.00±0.41 (n = 3)	–23.90 (n = 1)	
Largemouth bass	–25.94±0.73 (n = 9)	–23.93±0.71 (n = 6)	–25.26±1.00 (n = 10)			–22.55±0.19 (n = 4)	–21.93±0.68 (n = 3)		
Black crappie		–23.37±0.66 (n = 3)	–22.68±0.32 (n = 10)	–22.53±0.29 (n = 10)	–22.78±0.37 (n = 6)	–23.12±0.21 (n = 10)	–22.75±0.17 (n = 11)	–22.80±0.27 (n = 9)	–22.97±0.18 (n = 10)
Blue tilapia							–23.55±3.04 (n = 2)		
Spotted sunfish	–25.57±0.91 (n = 5)		–27.10±1.08 (n = 3)						

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Table A1 (*concluded*).

Species	Moore Haven, August	Cochran's Pass August	Cochran's Pass January	L005 August	L005 January	North Lake Shoal August	North Lake Shoal January	LZ40 August	LZ40 January
Dollar sunfish	–26.58±0.47 (*n* = 8)								
Bluespotted sunfish	–27.60±0.20 (*n* = 2)								
Eastern mosquitofish	–26.03±1.90 (*n* = 4)								
Least killifish	–24.14±2.59 (*n* = 5)								
Bluefin killifish	–26.79±0.62 (*n* = 7)								
Sailfin molly	–23.55±2.06 (*n* = 2)								
Striped mullet			–14.70 (*n* = 1)				–23.20 (*n* = 1)		

Table A2. Fish $\delta^{15}N$ ± 95% confidence level (*n* = number of individuals) for August 1996 and January 1997 by site.

Species	Moore Haven, August	Cochran's Pass August	Cochran's Pass January	L005 August	L005 January	North Lake Shoal August	North Lake Shoal January	LZ40 August	LZ40 January
Florida gar	9.55 (*n* = 1)	11.36±0.58 (*n* = 4)	12.19±0.91 (*n* = 10)	11.65±0.92 (*n* = 2)		11.87±0.92 (*n* = 5)	12.85±0.29 (*n* = 9)	13.65±0.45 (*n* = 9)	12.77±0.69 (*n* = 8)
Bowfin	10.32±0.19 (*n* = 6)		10.29±0.47 (*n* = 10)				11.23±1.12 (*n* = 3)		
Gizzard shad		8.34±0.89 (*n* = 2)	9.13±1.65 (*n* = 4)		7.50±0.51 (*n* = 10)	7.18±0.63 (*n* = 10)	10.25±0.43 (*n* = 4)		
Threadfin shad		7.67±1.34 (*n* = 3)		8.98±0.48 (*n* = 10)	9.39±0.48 (*n* = 10)				10.43±0.49 (*n* = 10)
Golden shiner	7.04±0.38 (*n* = 10)								
Lake chubsucker	6.97±0.23 (*n* = 10)		7.67±0.67 (*n* = 10)						
White catfish		10.84±0.33 (*n* = 10)		10.50±0.67 (*n* = 10)	9.90 (*n* = 1)	10.89±0.64 (*n* = 7)	10.47±0.61 (*n* = 6)	12.18±0.56 (*n* = 5)	12.14±0.41 (*n* = 9)
Brown bullhead		8.64±0.34 (*n* = 7)	8.43±0.57 (*n* = 3)	10.00 (*n* = 1)			10.30±1.64 (*n* = 3)		
Yellow bullhead	8.40 (*n* = 1)	10.40 (*n* = 1)	9.90±1.57 (*n* = 2)						

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Table A2 (*concluded*).

Species	Moore Haven, August	Cochran's Pass		L005		North Lake Shoal		LZ40	
		August	January	August	January	August	January	August	January
Channel catfish				8.53±0.23 (*n* = 10)		9.32±0.46 (*n* = 6)			
Tadpole madtom									11.30±0.98 (*n* = 2)
Chain pickerel	9.20 (*n* = 1)		9.00 (*n* = 1)				10.97±0.88 (*n* = 3)		
Atlantic needlefish					12.00 (*n* = 1)		12.70±0.59 (*n* = 4)		
Seminole killifish			7.98±0.49 (*n* = 5)						
Brook silverside	8.73±0.18 (*n* = 8)								
Warmouth	8.93±0.26 (*n* = 3)		9.56±0.37 (*n* = 10)						
Bluegill	9.73±2.30 (*n* = 2)	10.10±0.72 (*n* = 10)	8.97±0.40 (*n* = 10)			9.89±0.77 (*n* = 5)	9.68±0.52 (*n* = 4)		10.50±0.21 (*n* = 10)
Redear sunfish	8.48±0.62 (*n* = 11)	9.83±0.54 (*n* = 10)	8.46±0.41 (*n* = 10)	9.57±0.34 (*n* = 5)			10.63±0.66 (*n* = 3)	12.60 (*n* = 1)	
Largemouth bass	9.32±0.39 (*n* = 9)	10.83±0.12 (*n* = 6)	9.90±0.33 (*n* = 10)			12.23±0.38 (*n* = 4)	11.77±0.07 (*n* = 3)		
Black crappie		10.97±0.83 (*n* = 3)	11.66±0.56 (*n* = 10)	11.81±0.41 (*n* = 10)	12.02±0.26 (*n* = 6)	11.64±0.32 (*n* = 10)	12.06±0.27 (*n* = 11)	12.93±0.35 (*n* = 9)	12.14±0.28 (*n* = 10)
Blue tilapia							7.15±0.88 (*n* = 2)		
Spotted sunfish	9.86±0.40 (*n* = 5)		8.70±0.23 (*n* = 3)						
Dollar sunfish	7.73±0.46 (*n* = 8)								
Bluespotted sunfish	8.05±0.29 (*n* = 2)								
Eastern mosquitofish	7.60±0.81 (*n* = 4)								
Least killifish	7.20±0.44 (*n* = 5)								
Bluefin killifish	8.20±0.33 (*n* = 7)								
Sailfin molly	5.60±0.39 (*n* = 2)								
Striped mullet			12.90 (*n* = 1)			8.00 (*n* = 1)			

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Multispecies spatial assessment models for the British Columbia groundfish trawl fishery

Carl J. Walters and Ramón Bonfil

Abstract: A multispecies spatial model is proposed for evaluation of trawl management strategies and tested with data from British Columbia groundfish. Minimum stock sizes are estimated for 16 species using spatial catch per unit effort data; these data indicate that only small proportions of most stocks are exposed to fishing at any time and that exchange rates of fish between the grounds and other habitats are rapid. A gravity model for spatial effort allocation predicts substantial side effects of marine protected areas or discarding of particular species on nontarget species/grounds due to redistribution of fishing effort. Multispecies, multiground delay-difference models are used in conjunction with the gravity model for spatial effort distribution to predict long-term population responses to various regulatory strategies. This simulation suggests that species composition and spatial structure of the fishery are changing slowly due to reduction in abundance of long-lived species, but rapid collapses of target stocks are unlikely due to spatial redistribution of effort in response to local declines. We question whether quota management (individual vessel quotas) can be safely implemented due to extreme uncertainty about current stock sizes and suggest that a better strategy may be to simply denominate fishing rights as individual effort quotas while providing protection for sensitive stocks through carefully placed marine protected areas.

Résumé : Nous proposons un modèle spatial plurispécifique pour évaluer les stratégies de gestion des chaluts, modèle qui est testé avec des données sur le poisson de fond de la Colombie-Britannique. Nous estimons les tailles minimales des stocks de 16 espèces au moyen de données spatiales de prises par unité d'effort; ces données montrent que seules de petites proportions de la plupart des stocks sont exposées à la pêche en tout temps et que les échanges de poissons entre les bancs de pêche et d'autres habitats sont rapides. Un modèle gravitationnel de la distribution spatiale de l'effort prévoit que l'établissement de zones marines protégées ou le rejet d'espèces particulières aura des effets secondaires substantiels sur les bancs de pêche ou les espèces non visés, dus à la redistribution de l'effort de pêche. Des modèles à différences retardées visant plusieurs espèces et plusieurs bancs de pêche sont utilisés de pair avec le modèle gravitationnel pour la distribution spatiale de l'effort pour prévoir les réponses à long terme des populations aux diverses stratégies de réglementation. Cette simulation indique que la composition par espèces et la structure spatiale de la pêche sont en train de changer lentement en raison de la réduction de l'abondance des espèces qui vivent longtemps, mais il est improbable qu'on assiste à des effondrements rapides des stocks cibles vu la redistribution spatiale de l'effort en réponse aux déclins locaux. Nous nous demandons si la gestion des quotas (quotas individuels de bateau) peut être mise en oeuvre de façon sécuritaire en raison de l'incertitude extrême quant aux tailles actuelles des stocks et indiquons qu'il serait peut-être préférable de simplement définir les droits de pêche en termes de quotas d'effort individuels tout en protégeant les stocks sensibles par l'établissement de zones marines protégées bien situées.

[Traduit par la Rédaction]

Introduction

Multispecies trawl fisheries are characterized by harvesting a complex array of species over a mosaic of fishing grounds. Such species vary widely in productivity and distribution, and fishers have only limited capability to target particular stocks through selection of trawl depth and location. Despite widespread acceptance that multispecies fisheries require specific new integrative approaches for their assessment and management, most of these fisheries continue to be addressed using traditional single-species models. This paper reports the development of a multispecies spatial model and presents preliminary results for the British Columbia (B.C.) groundfish fishery.

The B.C. trawl fishery is a typical example of the complexities described above. Detailed information for stock assessment has been gathered for only a few major species/grounds, and only about half the current landings represent total allowable catches (TAC's) that can be set with confidence based on single species/stock analyses (Stocker and Fargo 1995). Measures have been taken to protect stocks for which there is very little information, particularly the many rockfish species that are likely unproductive. However, some measures like trip limits and local closures have encouraged discarding and misreporting of catches, further complicating the assessment problem (Richards 1994). There was a move to simplify regulations by setting multispecies combined TAC's

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and most recently individual vessel quotas (IVQ's) by species, and there has been a substantial improvement in information gathering with the mandatory observer program. There is a critical need for procedures to evaluate long-term impact on stock structure and productivity of management strategies like combined TAC's and IVQ's, and improved information gathering offers hope that this need can be met.

In this paper, we first use spatial statistics procedures with observer data for 1996 to develop catch rate distribution maps for the major species; these distributions are expanded by swept area estimates to provide minimum current biomass estimates for 16 major species. Spatial catch, effort, and biomass distributions are then used to divide the fishery into a set of relatively homogeneous, irregularly shaped fishing "grounds" where each ground represents an area within which fishers are unlikely to be able to fish selectively for particular species. We develop a model for predicting changes in distribution of fishing effort among these grounds in relation to changes in profitability (sum over species of catch rates times price, and cost factors specific to each ground) that might occur in the future due to changes in prices, local abundances, and regulations such as marine protected areas (MPA's). Finally we develop a multispecies, multiground delay-difference model for predicting local abundance responses to changes in fishing effort. This age–space structured model is capable of accommodating improved information on growth, natural mortality, recruitment variation, and dispersal among grounds as such information becomes available. Due to extreme uncertainty about current biomass and catchability for most species, so far we have used the multispecies, multiground simulation only to make general predictions about whether current distributions of fishing effort are likely to result in erosion of stock structure under multispecies combined quotas and whether spatial effort responses to changes in stock structure are likely to ameliorate or exaggerate the erosion process.

Methods

Notation

a_{ij} maximum age k_r recruits per unit spawning biomass
A_{a_j} fished area (square nautical miles)
A_{u_j} unfished area surrounding A_{a_j} where fish mix
b_{ij} local recruitment carrying capacity parameter
B_j biomass of all species on ground j
B_j^* biomass of all species on area A_{u_j}
B_{ij} FISHMAP biomass estimate for species i on ground j
$B_{ik,0}$ unfished biomass of species i on ground k
C_{ij} catch of species i on ground j
c_{ij} recruitment curve shape parameter
d_{jk} distance between the centers of grounds j and k
d_{bn} distance from block b to block n
D_e diversity in spatial effort allocation
D_j Shannon–Weiner species diversity index
D_i mean density of all fish species on ground j
D_{ij} mean density of fish i on and near ground j
D_j^* mean density of all fish species on area A_{u_j}
e_n observed effort in block n
$e_{j,t}$ effort on ground j during year t
E_j predicted effort on ground j
$\bar{E}_j$ average annual effort on ground j
E_{total} total effort over all grounds
F_{ij} fishing mortality rate of species i on ground j
i index for species
j index for grounds
k_r age of recruitment
K maximum biologically possible increase in mean recruitment rate per unit spawning biomass
K_s swept area per unit time
M_i natural mortality rate of species i
$M_{ijk,t}$ total number of adults or juveniles of species i moving from area j to area k in year t
m_j movement rate of fish onto area j
m_j' movement rate of fish off area j
$m_{ijk,t}$ proportion of species i moving from area j to area k in year t
n index for spatial blocks
N_{ij} number of fish of species i on ground j
P_j gross income per unit effort on ground j
P_0 a ground-independent base profitability at short-term effort equilibrium
p_i price per pound of species i
q_{ij} catchability of species i on ground j
$\bar{Q}_{ij}$ maximum likelihood estimate of $\ln(q_{ij})$
r_i base dispersal rate for species i
R_{ij} recruitment of species i on ground j
s_i dispersal distance scale parameter
$s_{ij,t}$ survival of species i on ground j during year t
$v_{ij,t}$ normally distributed observation errors
w_n weighting factor for catch per unit effort (CPUE) on block n
w_a body weight of fish at age a
w_j' updated attraction weights for effort
w_j attraction weights or empirical weight for cost of fishing on ground j
w_{k_r} body weight of fish at age of recruitment (w_{ik} for species i)
y_b^* weighted average CPUE in block b
$y_{ij,t}$ qualified CPUE of species i on ground j during year t
y_n observed CPUE in block n
Z total mortality rate
α Ford–Brody growth model constant
β proportionality parameter between CPUE and biomass
ρ Ford–Brody growth model slope
σ_d^2 index of local variance within block
σ_o^2 index of local variance between blocks
$\omega_{ij,t}$ recruitment anomaly for species i on ground j during year t

Estimation of spatial biomass distributions using FISHMAP

Georeferenced shot logs from the 1996 at-sea observer program and earlier logbooks are processed by FISHMAP (a Visual Basic 5.0 mapping application incorporating spatial statistics and available from the senior author) so as to provide an estimate of the spatial distribution of CPUE (pounds per trawl hour) for each major trawl species at a spatial resolution of 1 square nautical mile (1 nmi^2). Shot records are read into FISHMAP with spatial referencing to the nearest 1 nmi^2. Dividing the estimated CPUE for any 1-nmi^2 block by an estimate of the swept area per time trawling K_s (square nautical miles per hour of trawling, assumed to be 0.1 in default calculations) then provides a point estimate of the stock biomass in that 1-nmi^2 block. Summing these biomass estimates over space provides estimates of biomass by fishing ground (B_{ij} where i species and j is ground; see below) for use in spatial simu-

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lations and for comparison with biomass estimates from fishery-independent surveys and other assessment procedures. Provided we use a high K_s value in the calculation, and provided biomass estimates are assigned only to 1-nmi^2 blocks that were actually fished or were very close to blocks that were fished, this estimation procedure is expected to provide a very conservative estimate of stock biomass (the estimates do not include fish using areas that are not trawlable or fish off the bottom too far to be captured). In processing the CPUE data for each block, we assume that fishing is distributed at random with respect to the fish distribution within the block, i.e., that fishers are not able to selectively achieve higher catch rates than would be expected by chance at spatial scales below 1 nmi^2; we believe that this assumption is reasonable in view of the fact that most trawls are at least 2 nmi in length and hence will mostly sample at random even if the trawl starting point is specifically targeted on a local aggregation much smaller than 1 nmi^2 in size.

There are three key questions or uncertainties in the use of spatial CPUE analysis for biomass estimation. (*i*) What value should be assumed for the swept area per time fishing, K_s? (*ii*) For what collection of 1-nmi^2 blocks that were not fished (but were near fished areas) should CPUE estimates be provided by interpolation between, or extrapolation from, blocks that were actually fished (i.e., what is the total area of stock distribution to which the CPUE statistics should be applied; the same question applies in expanding survey data)? (*iii*) How should data from tows made at different times of year be combined, given that seasonal changes in both vertical and horizontal distributions may create high variation in K_s and also "smear" apparent distribution patterns (as migrating animals are pursued across blocks), given that there are not enough tows made in any short time period to permit separate mapping of densities by, say, months? We have answered these questions as follows for the analysis presented in this paper. (*i*) We present results only for the very conservative assumption $K_s = 0.1$ nmi^2/h (all fish between the otter boards caught, no fish in the water column above the net). (*ii*) We assume that fish could be present in all 1-nmi^2 blocks that were within 2 nmi of any block that was fished at any time during the year, i.e., we interpolate–extrapolate densities for all 1-nmi^2 blocks that were within 2 nmi in any direction from the blocks actually fished (interpolation–extrapolation procedure described below). (*iii*) We combine observations from all times of year, on the assumption that smearing effects due to migration (horizontal or vertical) will have balancing effects across blocks (movement from one block to another will cause the receiving block to have higher CPUE but the donor block to have correspondingly lower CPUE); examination of within-year patterns of fishing effort for the major grounds (e.g., Goose Island Gully) suggests that each area typically gets just a few major "pulses" of effort that are not clearly related to seasonal or spatial variation in CPUE. Further, we cannot detect local depletion of CPUE over small collections of the hardest fished blocks within grounds for any species during such pulses, indicating that there is considerable local mixing and movement among 1-nmi^2 blocks within each major fishing ground, on very short time scales.

Assumption *ii* above is clearly not a good one, and effects of this assumption may overwhelm errors due to incorrect specification of K_s. There are large areas likely occupied by various species that are not fished for economic and technical (tide, foul bottom) reasons. Further, the sizes of such unfished areas likely vary among stocks even within single species; for example, Pacific ocean perch (POP, *Sebastes alutus*) of the Moresby Gully stock likely occupy a much larger area of unfishable ground (e.g., areas of strong tidal current near Cape St. James) than do POP of the Goose Island Gully stock. This means that even within-species comparisons of spatial CPUE patterns among grounds or stocks must be treated with great caution; we cannot, for example, safely use the effective survey catchability estimated from age-structured population analysis for POP in Goose Island Gully (around $0.2K_s$, Richards and Olsen 1996) to interpret or expand CPUE data for POP in Moresby Gully.

For both fished and unfished 1-nmi^2 blocks, we take the best estimate of CPUE for the block to be a spatially weighted average of the CPUE in that block and in surrounding blocks within a 2-nmi radius (a "potential mapping" approach, Kulka et al. 1996). If y_b^* is the weighted average CPUE in block b and if y_n ($n = 1,..., 25$) are the observed CPUE's (total catch divided by total effort) in the blocks within 2 nm of (and including) block b, we estimate y_b^* as

$$(1) \qquad y_b^* = \frac{\sum_n y_n w_n}{\sum_n w_n}$$

where the weights w_n are calculated as

$$(2) \qquad w_n = 1/[\sigma_d^2 d_{bn} + \sigma_o^2/e_n]$$

where σ_d^2 is an index of local variance (within block), e_n is effort in block n, σ_o^2 represents variance between blocks (variance in prediction of block b CPUE from block n), and d_{bn} is distance (nautical miles) from the center of block n to the center of block b ($d_{bn} = 1$). Equation 2 is simply an inverse variance weighting function (a simple form of variogram) that assigns weights to data from cells surrounding cell b that are inversely proportional to the distances of these cells from b but proportional to effort e_n in those cells (somewhat more weight on estimates y_n from cells that had higher efforts and hence presumably more accurate y_n estimates). We assumed $\sigma_d^2 = 100$ (based on typical variability in CPUE for heavily fished blocks) and $\sigma_o^2 = 1000$, although we found the spatial CPUE patterns (and summed abundance estimates) to be largely insensitive to these values over ranges of 10–500 for the former and 200–5000 for the latter.

Prediction of changes in species composition due to selection of alternative fishing grounds

As species and stock composition of the groundfish community varies in response to environmental variables and harvesting, fishers will respond by varying fishing practices so as to maintain highest possible rates of economic return to effort. The primary factor that they can vary is location of fishing, or grounds, where they expend effort. Based on 1996 observer data, there are only a quite limited number of distinctive grounds where effort can concentrate, defined by spatial region and depth. Each such ground apparently has distinctive species composition.

We model changes in catch composition, and hence variable exploitation rates, by using a "gravity model" for the distribution of effort among grounds. In gravity models, the share of total effort allocated to each ground is assumed proportional to the relative economic "attractiveness" of that ground, where attractiveness is in turn proportional to the expected profitability of the ground as measured both by availability of fish and by a complex collection of fish availability and cost factors. Gravity models were first proposed for effort prediction by Caddy (1975). Alternative, more complex methods are suggested in Hilborn and Walters (1987). Mathematically, a gravity model predicts effort expended on ground j, E_j, as

$$(3) \qquad E_j = \frac{w_j P_j}{\sum_k w_k P_k} E_{\text{total}}$$

where w_j is an empirical weight representing relative cost of fishing on ground j, E_{total} is total effort over all grounds, P_j is gross income per unit effort on ground j calculated as

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Table 1. Estimates of growth and survival parameters used for delay-difference simulation of multispecies, multiground changes in the B.C. trawl fishery and corresponding F_{opt} estimates.

	Delay-difference model parameter				Recruitment		
Groundfish species	α	ρ	w_k	e^{-M}	K	Age k	Derived F_{opt}
Dogfish	0.171	0.979	1.528	0.950	5	18	0.035
Pacific cod	1.032	0.992	2.400	0.522	5	3	0.239
Rougheye	0.093	0.929	0.619	0.950	5	16	0.043
Perch	0.093	0.929	0.619	0.950	5	9	0.043
Shortraker	0.093	0.929	0.619	0.950	5	16	0.043
Silvergray	0.337	0.851	1.620	0.860	5	12	0.119
Yellowtail	0.337	0.851	1.842	0.860	5	9	0.119
Canary	0.475	0.845	2.593	0.900	5	12	0.095
Yellowmouth	0.093	0.929	0.619	0.950	5	16	0.043
Shortspine	0.450	0.998	0.328	0.910	5	20	0.036
Longspine	0.007	0.962	0.075	0.920	5	15	0.064
Blackcod	0.719	0.856	4.000	0.920	5	5	0.076
Lingcod	1.854	0.963	3.643	0.779	5	4	0.111
Rock sole	0.181	0.904	0.515	0.778	5	4	0.133
Dover sole	0.127	0.936	0.414	0.860	5	4	0.084
English sole	0.146	0.868	0.329	0.800	5	5	0.120

Note: Shaded areas show initial parameter guesses based on other species; F_{opt} is the annual exploitation rate expected to give MSY over the long term.

$$(4) \qquad P_j = \sum_i q_{ij} B_{ij} p_i,$$

q_{ij} is catchability of species i on ground j, B_{ij} is stock biomass of species i on ground j, and p_i is price per pound of species i. The effort distribution model eq. 3 allocates an assumed total effort E_{total} using ratios $w_j P_j$, where P_j in turn depends on catchabilities, biomasses, and prices of all species i occurring on each ground j. As biomasses B_{ij} and prices p_i vary, so will the predicted efforts allocated to the grounds. Further, we can vary catchabilities q_{ij} to represent factors such as local closures (MPA's). By computing effort allocations on relatively short time steps within each simulated fishing season, we can account for species quotas by either (*i*) setting prices to zero in situations where quotas are exceeded, so that the simulated catches arising from E_j and q_{ij} are effectively "dumped" by the fishers, or (*ii*) closing the ground to fishing by setting $P_j = 0$.

Equation 3 can be derived from two key assumptions and is not merely a mathematically convenient or intuitive method for predicting allocation of effort among fishing grounds. First, fishing grounds contain only a small part of the harvestable stock at any moment, with this exposed biomass varying over short times due mainly to spatial mixing processes and local depletion. Secondly, fishers redistribute effort over grounds so that no ground stands out in terms of profitability (grounds with high profitability are fished harder to drive down local density of fish; fishers avoid grounds with low profitability). This "ideal free distribution" (Gillis and Peterman 1998) derivation is presented in Appendix 1.

Estimation of parameters for the effort distribution model requires four steps: (*i*) divide the coast into relatively homogeneous grounds (depth, area) that can be identified from the 1994–1996 logbook data using FISHMAP, (*ii*) again using the 1994–1996 logbook data and FISHMAP, estimate C_{ij} (catch of species i on ground j), $\overline{E}_j$ (average annual effort on ground j), B_{ij} (FISHMAP biomass estimate from spatial CPUE and swept area analysis), and $q_{ij} = (C_{ij}/\overline{E}_j)/B_{ij}$, (*iii*) using price per pound data for each species, compute a mean historical profitability P_j for each ground j from eq. 4 and the B_{ij} and q_{ij} estimates from step *ii*, and (*iv*) estimate the relative attraction weights w_j from historical efforts $\overline{E}_j$ (step *ii*) using the following simple iterative procedure: (*a*) set all w_j initially to 1.0, (*b*) calculate an updated estimate w'_j for each w_j from the equation

$$(5) \qquad w'_j = \frac{\sum_k w_k P_k - w_j P_j}{P_j(E_{total}/\overline{E}_j - 1)},$$

and (*c*) set $w_j = 0.5w_j + 0.5w'_j$ and return to step *b* until w_j estimates stop changing (this iterative procedure generally converges within five iterations and need only be done once before starting a simulation).

An important point about the iterative procedure in step *iv* is that it provides an attraction weight for each ground that ensures that the ground will have exactly the same simulated fishing effort from eq. 3 as was observed in 1996, provided the simulated profitabilities of all grounds P_j are the same as the observed profitability in 1996 and provided the simulated total effort is the same as in 1996. The simulated effort distribution among grounds will differ from the 1996 observed distribution only if simulated profitabilities change due to changes in abundance patterns, prices, and catchabilities q_{ij}.

The catchabilities q_{ij} by species and ground resulting from step *ii* above are likely to give gross overestimates of local fishing mortality rate $F_{ij} = q_{ij}B_{ij}$ if B_{ij} is taken to be the total stock potentially exposed to fishing on ground j rather than the fishable stock "seen" in the FISHMAP analysis of areas actually fished. Suppose the FISHMAP estimate of mean density on (and near) a ground is D_{ij} (tonnes per square nautical mile), implying spatial mean $CPUE_{ij} = K_s D_{ij}$ over a fished area A_{a_j} nmi^2 (B_{ij} from FISHMAP is $D_{ij}A_{a_j}$). Suppose fish on the ground are mixing with fish from a surrounding "fish-shed" area of A_{u_j} nmi^2 (or from the water column above), where densities average D^u_{ij} t/nmi^2. Then the actual stock exposed to fishing impact on the ground is $B'_{ij} = D_{ij}A_{a_j} + D^u_{ij}A_{u_j}$. If q'_{ij} is defined as the catchability for this larger stock (so $CPUE_{ij} = q'_{ij}B'_{ij}$), then q and q' are related by $q'_{ij} = q_{ij}/[1 + (D^u_{ij}A_{u_j})/(D_{ij}A_{a_j})]$, i.e., q' for the whole local stock is smaller than q by a "vulnerability factor" equal to 1 plus the ratio of the unfished to exposed biomasses. The estimation of these vulnerability factors for stocks/species lacking good biomass estimates from traditional single-species assessment

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methods is perhaps the single biggest challenge for groundfish scientists today in B.C.

We used effort and species distribution maps from the 1996 logbook data to define a set of 19 major fishing grounds. These grounds can be further refined and subdivided for future analysis using mouse "sketching" procedures in FISHMAP.

Delay-difference model for simulation of multispecies, multiground harvest impacts

To evaluate potential for long-term "erosion" in the species/ground structure of the trawl fishery under regulations that permit (or force) effort movement among grounds, we have developed an age-structured model based on the Deriso–Schnute delay-difference relationships for stock biomass and numbers (Deriso 1980; Schnute 1985). The main assumption in these relationships is that there is knife-edge recruitment at age k_r (recruitment age) to the exploitable biomass, with annual survival rate $s_{ij,t}$ (where i is species, j is ground, and t is year) being independent of age for animals aged k_r and older. It is also assumed that body growth for age k_r and older animals is well described by the Ford–Brody relationship $w_{a+1} = \alpha + \rho w_a$ where w_a is weight at age a (this relationship almost always works very well provided k_r is beyond the age of growth inflection, which is the case for all important species in the B.C. trawl fishery). Under these assumptions, the exploitable biomass $B_{ij,t}$ for species i fish on ground j in year t and total exploitable numbers of fish $N_{ij,t}$ would be expected to vary in the absence of mixing between grounds as

$$(6) \qquad B_{ij,t+1} = s_{ij,t}(\alpha_i N_{ij,t} + \rho_i B_{ij,t}) + w_{k_r} R_{ij,t+1}$$

$$(7) \qquad N_{ij,t+1} = s_{ij,t} N_{ij,t} + R_{ij,t+1}$$

where $R_{ij,t+1}$ is the number of age k_r recruits to ground j in year $t+1$. These very simple equations generally describe the biomass and numbers dynamics of age-structured populations very well, even when recruitment is not knife edge at age k_r, provided good predictions are possible for the annual survival rate s_t and recruitment rate $R_{ij,t+1}$.

We assume that survival rate will vary mainly due to independent effects of natural mortality rate M_i and fishing mortality rate $F_{ij,t} = q_{ij}E_{j,t}$ (where $E_{j,t}$ is effort on ground j in year t) as

$$(8) \qquad s_{ij,t} = \exp(-M_i - F_{ij,t}).$$

The main causes of poor predictions from eq. 8 are likely to be density–time dependence in catchability q_{ij} and (or) incorrect prediction of the ground fishing efforts $E_{j,t}$. We predict $E_{j,t}$ using the effort allocation model described above, and we do not account for local density dependence or technological growth in q_{ij} (the main cause of density dependence in q is spatial concentration of fish, and we hope that the use of relatively small fishing grounds makes it reasonable to assume random search within each ground; note that q_i averaged over areas j may well show overall density dependence if effort becomes progressively concentrated on remaining productive grounds over time as fish are lost from other grounds).

Recruitments $R_{ij,t}$ are assumed to depend on local stock biomass $B_{ij,t}$ and on environmental effects $\omega_{ij,t}$ according to a Shepherd (1982) stock–recruitment relationship:

$$(9) \qquad R_{ij,t+k_r} = a_{ij}B_{ij,t}/(1 + a_{ij}b_{ij}B_{ij,t})^{c_{ij}} \exp(\omega_{ij,t})$$

where a_{ij} is maximum age k_r recruits per unit spawning biomass, b_{ij} is a local recruitment carrying capacity parameter, and c_{ij} is a recruitment curve shape parameter (we use $c_{ij} = 1$, implying a Beverton–Holt recruitment curve shape).

Unfortunately, we can only estimate the pattern of environmental effects $\omega_{ij,t}$ from historical data for a few species in a few areas where age composition data have been gathered regularly (POP in Goose Island Gully, Pacific cod (*Gadus macrocephalus*) in Hecate Strait and west coast Vancouver Island, English sole (*Pleuronectes vetulus*) and rock sole (*Pleuronectes bilineatus*) in Hecate Strait). For initial evaluations of potential stock structure changes, we have assumed $\omega_{ij,t} = 0$ (deterministic stock–recruitment analysis) for other stocks and have compared such predictions with simulations with $\omega_{ij,t}$ normally and independently distributed (lognormal recruitment variation such that recruitment is mainly low with occasional very strong year classes). To estimate the a_{ij} and b_{ij} parameters, we first assume that each ground had a sustainable, natural biomass $B_{ij,0}$, and we treat this biomass as a key leading parameter. Sustainability of $B_{ij,0}$ implies on average (from eqs. 6 and 7) that we can calculate average unfished recruitment rates $R_{ij,0}$ from

$$(10) \qquad B_{ij,0} - s_{ij,0}B_{ij,0}(\alpha_i/w_{i,0} + \rho_i) = w_{k_r}R_{ij,0}$$

where $s_{ij,0} = \exp(-M_i)$ and $w_{i,0}$ is unfished average body weight, given by (see Hilborn and Walters 1992; Schnute and Richards 1998)

$$(11) \qquad w_{i,0} = [s_{ij,0}\alpha_i + w_{ik}(1 - s_{ij,0})]/(1 - s_{ij,0}\rho_i).$$

The average natural recruitment rate $R_{ij,0}$ from eq. 10 implies one point on the recruitment curve, from which we can calculate b_{ij}, given assumed a_{ij} and c_{ij}, as

$$(12) \qquad b_{ij} = 1/(B_{ij,0}a_{ij})\{[a_{ij}w_{i,0}/(1 - s_{ij,0})]^{1/c_{ij}} - 1\}.$$

The key issue then becomes to assess the recruitment curve slope a_{ij} at low stock biomass, i.e., the "risk" of recruitment overfishing as B is reduced from $B_{ij,0}$. The only empirical way to obtain this parameter is dangerous overfishing, and it is prudent to make some reasonable prior assumption about it that will not encourage overfishing in the first place. We take a very conservative approach to estimation of a_{ij}; we assume it to be

$$(13) \qquad a_{ij} = KR_{ij,0}/B_{ij,0} \quad \text{where } 5 < K < 10.$$

Here, the compensation parameter K represents the maximum biologically possible increase in the mean recruitment rate per unit spawning biomass, hence expressing a_{ij} as an increase relative to the base recruits/spawner ratio $R_{ij,0}/B_{ij,0}$ estimated for the unfished stock. Empirical studies and reviews like Myers and Barrowman (1996) and Myers and Mertz (1997) usually suggest $K > 5$ to 10; very high K values imply recruitment independent of stock size (if $c = 1$) over a wide range of stock sizes, while K values near 1.0 imply recruitment proportional to spawning biomass. Our default assumption $K = 5$ leads to extremely conservative estimates of the fishing mortality rate F_{opt} that would give maximum sustainable yield (MSY) (Table 1), generally much lower than the $F_{opt} \approx M$ that commonly results from analyses such as assuming $F_{opt} \approx F_{0.1}$. For example, $K = 2$ for POP implies $F_{opt} \approx 0.015$, i.e., about $0.3M$, which is substantially lower than even the empirical Patterson (1992) finding for pelagic stocks that $F_{opt} \approx 0.6M$.

Parameter estimation for the basic model without dispersal involves two steps: (*i*) estimation of α_i, ρ_i, w_{ik}, and M_i from data on growth and longevity and (*ii*) estimation of unfished biomasses $B_{ij,0}$, from which the recruitment parameters a_{ij} and b_{ij} are derived using the sustainability assumption. Unfortunately, even the growth–longevity parameters can be estimated for only a few groundfish species with available B.C. data; for species lacking basic age composition data (mainly rockfishes), we have assumed values either from U.S. assessments or from a conservative assumption of slow growth and high longevity (Table 1).

For few species like POP and Pacific cod, we can obtain $B_{ij,0}$ estimates for major grounds from other assessments (Haist and Fournier 1996; Richards and Olsen 1996) and (or) directly fitting the model to survey or CPUE time series. But for most species and

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grounds, we are exploring two alternative estimation procedures to obtain the vulnerability factors defined above. The first of these is based on starting simulations before the trawl fishery began, with progressively larger $B_{ij,0}$ values until the model produces current biomasses near FISHMAP $B_{ij,1996}$ values expanded by reasonable guesses at vulnerability factors to account for likely $K_v < 0.1$ and unfished area effects. Variants of this procedure involve "driving" the model with total historical trawl efforts, letting the model internally allocate these efforts to the simulated grounds. This procedure is obviously suspect, since historical effort distributions have certainly been influenced by various changes in technology, relative prices of the species, and regulations such as trip limits on particular species. A key concern with this approach is that it is very difficult to account for all historical changes in prices and technology, so in particular, we may overestimate historical fishing on some areas that were not harvested until recently.

The second estimation procedure (details in Appendix 2) is based on treating each of the grounds as a unit stock and then fitting the delay-difference model to qualified CPUE, survey data, and FISHMAP estimates for each stock/ground combination while driving the model with historical catches for the grounds. This method amounts to assuming constant catchability over time and using CPUE trends to provide information about whether stock sizes are now stable, declining, or increasing by ground. This method uses the FISHMAP biomass estimates only to help limit the range of probable unfished biomasses, but suffers from other obvious weaknesses including difficulties in attributing historical effort and catch to stocks within grounds (changes in targeting practices within areas), failing to account for increases in q due to range collapse and improvements in fishing power over time, and risk of "double-accounting" for fish outside the areas fished (i.e., estimating q so as to include fish in two or more statistical areas that in fact represent single pools that contribute to catch in both areas).

In the delay-difference assessments presented below, recruitment anomaly data are included for only a few species and only at the species level (same sequence for all grounds); use of species-level anomaly patterns appears justified for Pacific cod (Hecate Strait and west coast Vancouver Island patterns quite similar) and POP (strong year classes in the same years for Moresby and Goose Island gullies) and cannot yet be tested for other species. In principle, it is possible to estimate recruitment anomaly sequences directly for the delay-difference model from relative abundance time series data using the Walters (1995) dynamic programing method; however, we would have to use mainly CPUE data, and we believe that recruitment anomaly effects in these data are badly confounded with effects of various environmental and technological factors on catchability.

For long-term evaluations of changes in stock structure, it may be critical to account for dispersal/migration between fishing areas. Mixing of fish within grounds is certainly important, as evidenced by lack of local depletion during periods of peak effort on intensively fished grounds; most likely, this mixing extends to larger scales as well. Mixing has obvious implications for the efficacy of MPA's as a method to protect breeding stocks, but it is not obvious how mixing will interact with spatial redistribution of effort to either enhance or prevent erosion of stock structure. To provide at least a crude capability to evaluate possible impacts of mixing between grounds, we allow the capability to separately model exchange rates of prerecruits and adults using a simple linear model of the form

$$(14) \quad M_{ijk,t} = m_{ijk} N_{ij,t}$$

where $M_{ijk,t}$ is the total number of adults or juveniles of species i moving from area j to area k in year t and the proportion moving m_{ijk} is specified as a function of distance between j and k and relative stock size in area k by the relationship

$$(15) \quad m_{ijk} = r_i \frac{\exp(-s_i d_{jk}) N_{ik,0}}{\sum_l \exp(-s_i d_{jl}) N_{il,0}}$$

where r_i is the base dispersal rate for species i, s_i is a dispersal distance scale parameter (smaller values imply longer dispersal distances), d_{jk} is the distance between the centers of grounds j and k (nautical miles), and $N_{ik,0}$ is the unfished biomass of species i on ground k, as above.

This formulation allows us to specify alternative hypotheses about propensity to move (r_i values) and likely distances travelled (s_i) and includes the assumption that areas with higher natural biomass are likely to be larger and hence to be more likely to be encountered and used by dispersing individuals. Note that the ratio in eq. 15 can be viewed as an attractiveness for area k for animals dispersing from area j divided by the sum of such attractivenesses over all areas l to which animals from area j might disperse. Thus, eq. 15 breaks the dispersal prediction into two parts: (*i*) how many fish move and (*ii*) where they are likely to end up. A problem with the formulation is that it does not ensure stability of the $B_{ij,0}$ values for high r_i, i.e., simulated stock structure may change due to imbalances in movement between areas, even in the absence of fishing. The only way we can see to avoid this problem for high-r_i scenarios is to allow r_i to vary with j such that emigration rates are varied between grounds so as to ensure immigration–emigration balance for every ground in the absence of fishing; various statistical criteria could be used to ensure that the resulting e_{ij} are "close" to an overall r_i target rate. We have not yet attempted to code algorithms for such balancing and have restricted test scenario development to cases where the r_i are low enough to avoid large changes in $B_{ij,t}$ in the absence of fishing (e_i values as high as 0.3 do not appear to cause noticeable imbalance for most species examined so far with the model). Also, this method for estimating m_{ijk} assumes that every ground pair j,k in fact has suitable habitat (depths, etc.) for species i; the calculation could easily (but tediously) be refined to exclude particular unlikely movements (e.g., into shallows for deepwater species), but such refinements would not affect basic predictions about effect of movement in general.

To provide a flexible framework for future policy analyses and data analyses, we have implemented the multispecies, multiground delay-difference model and effort gravity model in a Visual Basic 5.0 application called EFFMOD (available from the senior author). EFFMOD first loads historical effort and catch statistics for 1954–1996 and data from FISHMAP for calculation of effort response and current stock size parameters. It then offers options for model fitting and simulation; fitting options include varying species B_0 values to try and match multiples of 1996 FISHMAP biomass estimates and the single-stock method detailed in Appendix 2. Simulation gaming is facilitated by a policy interface that allows specification of four types of effort and quota policies. First, coastwide effort can be varied to represent alternative fleet size policies. Second, individual fishing grounds can be permanently closed as MPA's. Third, a separate catch quota or TAC can be set for each species on each ground, with any catch above this quota discarded. Under this option, annual effort is calculated with a sequential algorithm that allocates effort until the first quota limit is hit, and then, ground profitabilities are recalculated omitting the limiting species; this process of testing for next quota limit and then recalculating the spatial effort distribution is repeated until all effort for each year has been allocated. The fourth option is similar to the third, i.e., a separate quota or TAC can be set for each species/ground, but additionally, each ground is closed to fishing (effort attractiveness set to 0.0) for the rest of the simulated year when the first species quota for it is reached. The fourth option represents a "weakest stock" management strategy, and it can well result in reduction of total effort in simulated years when grounds are closed before the total potential effort is allocated.

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The sequential effort allocation algorithm can also be used to simulate impacts of combined species quotas over larger regulatory or statistical areas. These areas are defined for each simulation run by assigning each ground a regulatory area index; hence the regulatory areas need not correspond to historical statistical areas or grounds. However, we doubt that such quotas would be wise (see the Discussion section below).

Besides the usual catch and stock size predictions, the simulation provides two output indices of change in overall biological diversity and diversity of fishing opportunities. For each fishing ground j each simulated year, the model calculates the Shannon–Weiner species diversity index $D_j = -\Sigma_i(B_{ij}/B_j)\log(B_{ij}/B_j)$, where B_j is total biomass of all species i on ground j. Each year, diversity in spatial effort allocation is measured by $D_e = -\Sigma_j(E_j/E_{total})\log(E_j/E_{total})$. These diversity measures can vary in complex ways. For example, increases in total fishing effort can cause D_e to increase by depressing abundance in favored grounds so that effort spreads out more to other grounds. Likewise, biomass diversity can decrease in some grounds due to reduction in less productive species but increase in others due to selective reduction of species that are initially dominant (e.g., POP in Moresby and Goose Island gullies).

Preliminary results from the multispecies assessment model

FISHMAP biomass estimates

Application of the spatial averaging method of eqs. 1 and 2 to the 1996 observer data shows that major groundfish species have fascinating spatial distribution patterns, with abundance for each species most often concentrated in a few local grounds and (or) over a narrow depth range (Fig. 1). Fishing mortality rate, as indicated by swept area per square nautical mile (K_s × effort hours), is also highly concentrated (Fig. 2); only about 900 of the 6272 1-nmi^2 blocks fished receive half the total effort. Coastwide minimum biomass estimates (CPUE/K_s, summed over all 1-nmi^2 blocks) are small compared with catches for most species (Table 2), implying unrealistically high estimates of fishing mortality rate F (catch/biomass) for most species; similar results have been obtained in comparisons of biomass estimates for POP from survey CPUE and K_s (Yamanaka et al. 1996) with biomass estimates from modelling (Richards and Olsen 1996). Note that no variances are provided for the stock size estimates in Table 2; variance estimates based on variation in catch rates within the area fished would grossly underestimate uncertainty about total biomass, which comes mainly from uncertainty about the proportion of the stock "visible" to sampling. Considerable interannual variation in the estimates is evident in Table 2, most likely reflecting interannual variation in fish distributions relative to fishing grounds. Note that biomass estimates for a few rockfish stocks (shortraker (*Sebastes borealis*), silvergray (*Sebastes brevispinis*), canary (*Sebastes pinniger*)) show alarming declines from 1994 to 1996, but these apparent declines are substantially larger than can be accounted for by catches and hence most likely represent interannual variation in fish distributions rather than real abundance changes.

Is it possible that the biomass estimates in Table 2 are actually overestimates for at least some stocks, rather than gross underestimates as we would suspect from independent assessments? Local fish densities could be overestimated if there were highly nonrandom effort distributions at spatial scales smaller than 1 nmi^2. For example, suppose all the fish of some stock were concentrated in a 0.1-nmi-wide band crossing a 1-nmi^2 block (fishers do say that they target such bands in a few places, like a Y-shaped trawl "path" in Moresby Gully, Fig. 3) and that all trawls in the block were accurately placed within this band. Then, we would overestimate density for the block as a whole 10-fold if we applied the mean CPUE to a 1-nmi^2 area rather than the 0.1-nmi^2 area from which it was actually taken. Indeed, it is precisely this sort of concern that leads to the need for spatial CPUE analysis in the first place. Fortunately, when we examine precise trawl locations within most 1-nmi^2 blocks, we do not see such nonrandom set patterns. For example, Fig. 3 shows set start points for 1996 trawls in one of the most worrisome areas of the coast, the Moresby Gully Y path. In this area, there are a few heavily fished 1-nmi^2 blocks within which we can see nonrandom search patterns, but even for these blocks, roughly half the area is fished so that the upward density bias due to assuming the whole 1 nmi^2 was fished would only be a factor of 2. In short, biases due to local nonrandomness in trawl sampling pale into insignificance compared with uncertainty about abundance in blocks that were not sampled at all.

To evaluate effects of aggregating data over time, we did a simpler spatial analysis for each month of the 1996 data set in which we simply calculated average CPUE by larger (3 × 3 nmi, 9 nmi^2) blocks fished during the month and estimated biomasses as the sum of these block means times $9/K_s$. This procedure revealed strong seasonality in biomass estimates for key species like POP but with annual averages for the seasonal estimates that are mainly quite close to the annual estimates from the more complex spatial averaging procedure. Similarity in these estimates indicates that the annual estimates are not biased upward greatly by including only high CPUE observations (due to fishers targeting on specific blocks only at times when densities of particular species are high in those blocks), further reinforcing our contention that the spatial estimation procedure provides a minimum biomass estimate for most species.

The spatial density and effort patterns in Figs. 1 and 2 were used to sketch a set of relatively homogeneous fishing grounds (Fig. 4). In many cases, these correspond closely to minor statistical areas used for past reporting and assessments, but in some areas (e.g., off Vancouver Island), our ground definitions aim to account for strong depth gradients.

The grounds defined in Fig. 4 have highly variable sizes and distinctive catch species compositions, but mainly relatively similar profitabilities (P_j, sum over species of price × mean CPUE). As predicted from the gravity model derivation in Appendix 1, the attraction weights w_j are more variable (Table 3). This result for P_j and w_j is encouraging: had we found many grounds with apparently high profitability but low effort (low w_j) or vice versa, we would be seriously concerned about whether the gravity model formulation is at all capable of predicting spatial effort patterns. Relatively even profitability over the grounds indicates that fishing has eliminated any extremely profitable situations over the years (any grounds with extremely high profitability have long since been found and depleted to the point where they are about as profitable as other grounds). Continuing high efforts in a few grounds with apparently low profitability may

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Fig. 1. Spatial distributions of annual average CPUE for major bottom trawl species along the B.C. coast from the 1996 observer data. CPUE are interpolated–extrapolated for 1-nmi^2 cells that were not fished (but were within 2 nmi of fished cells) using the weighted averaging procedure described in the text. Areas of relatively high density are shown in black.

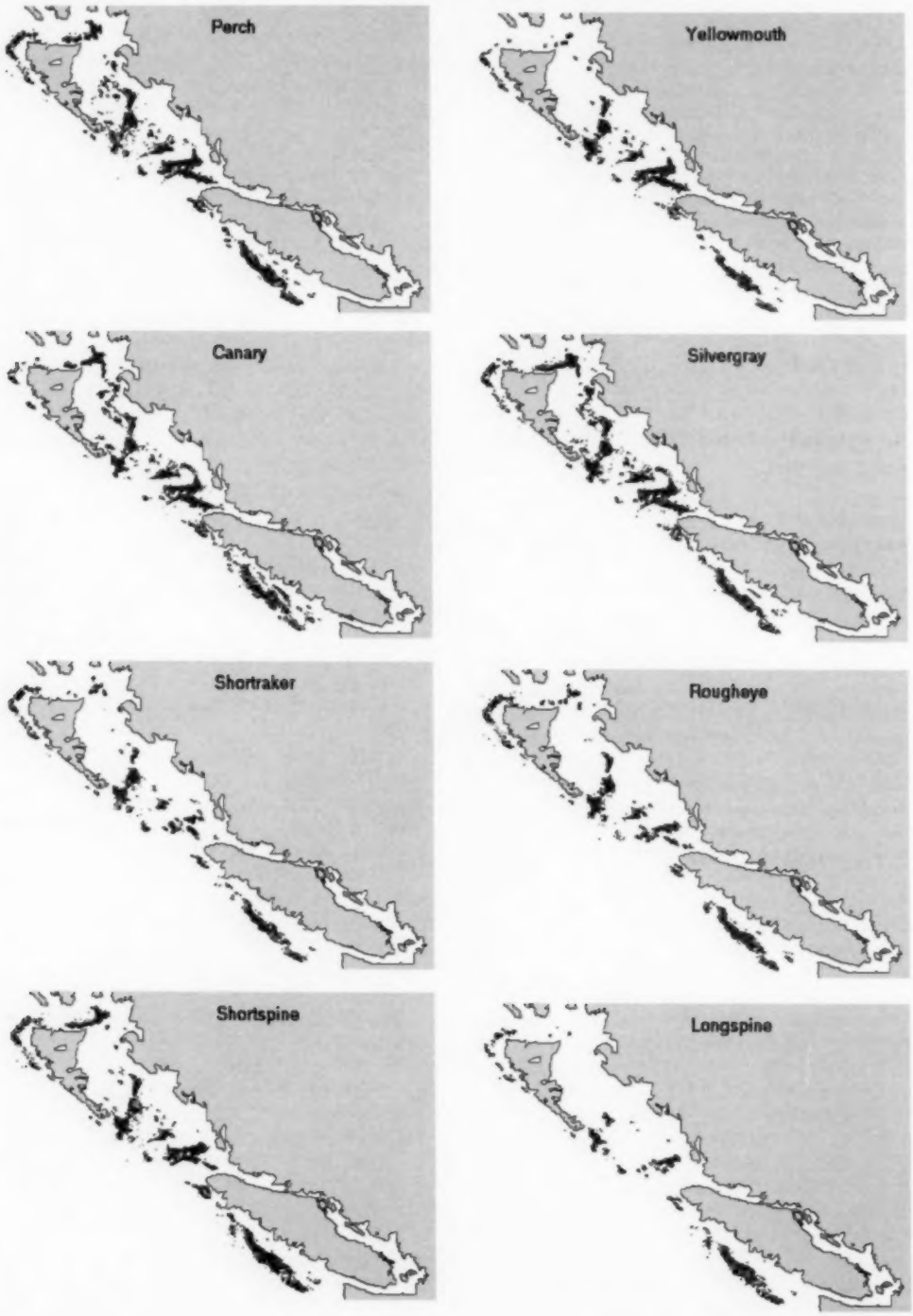

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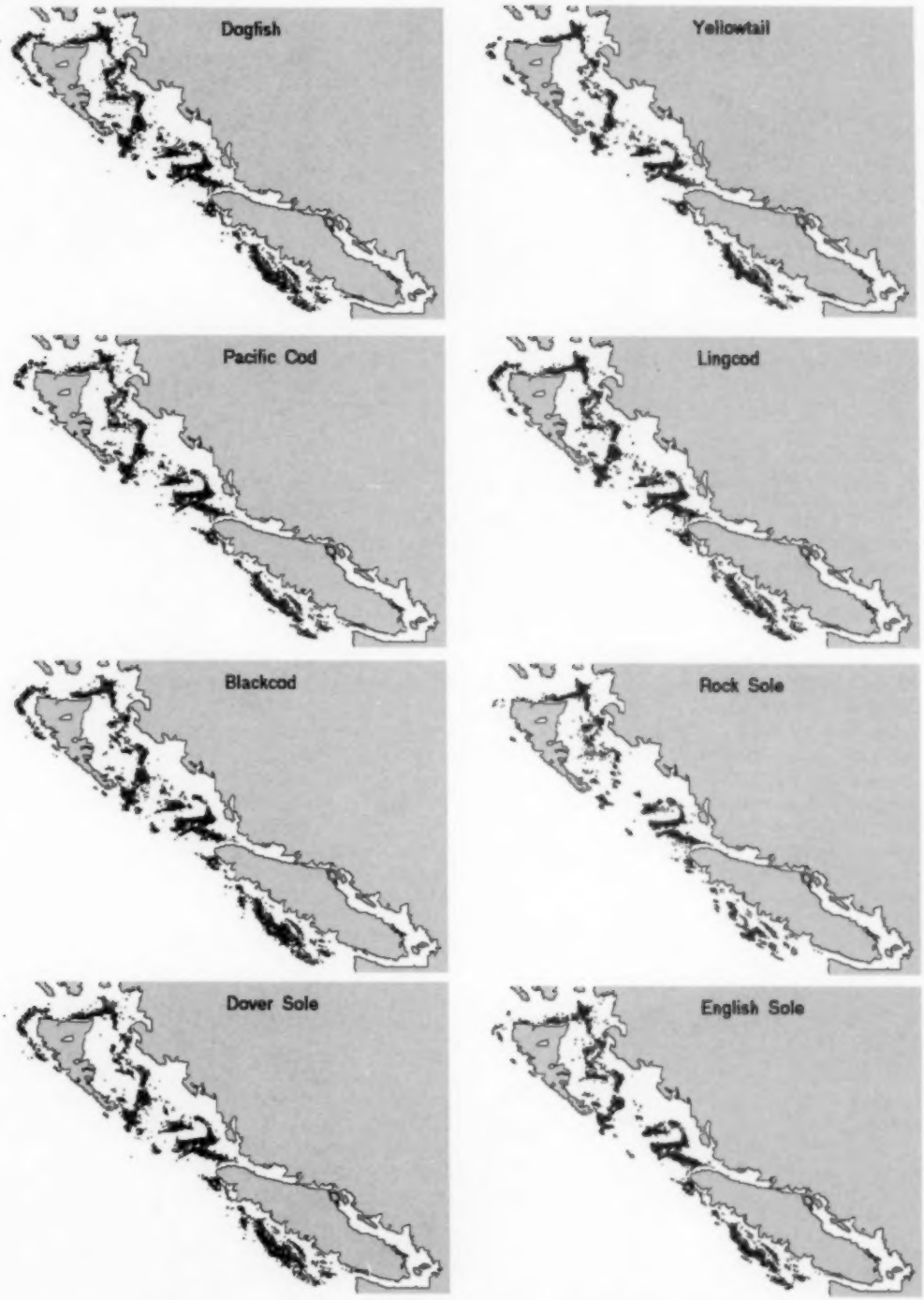
Fig. 1 (*concluded*).



reflect low fishing costs on such grounds, a difficult effect to quantify (the effect of variable cost is implicitly included in the "empirical" w_j estimates). Also, persistence today of very profitable grounds would have to be due to extremely high immigration rates of fish onto such grounds, in view of the high fishing rates (swept area) seen today on preferred grounds (Fig. 2). One cause for concern is that weights estimated from the 1994–1995 volunteer logbook data do not agree

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Fig. 2. Spatial distribution of bottom trawl effort on the B.C. coast from the 1996 observer program. Black shading indicates areas of high fishing effort with swept area F approaching 1.0 (nmi^2 swept/nmi^2 ground = 1.0) assuming that area swept per hour K_s = 0.1 nmi^2.

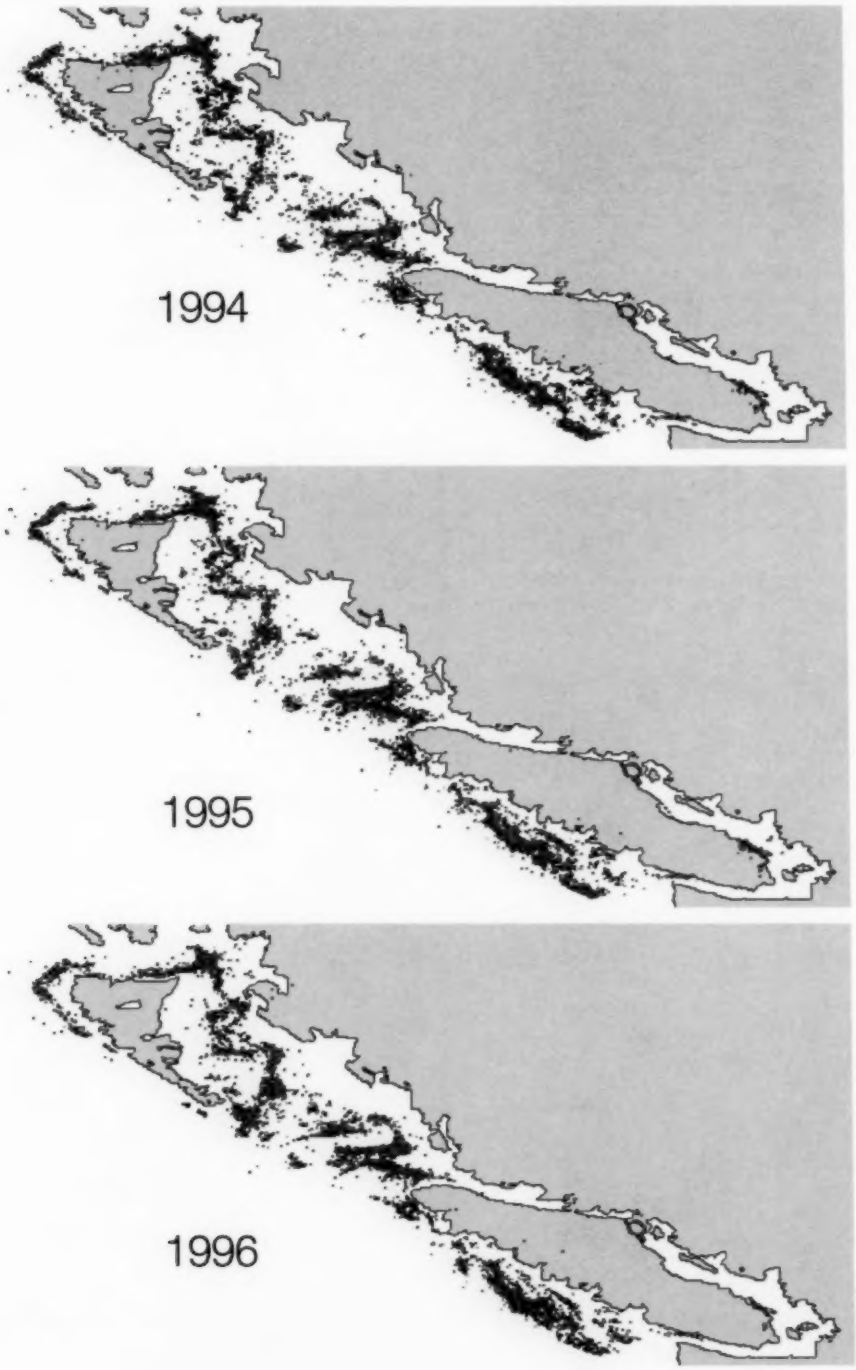

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Table 2. FISHMAP estimates of total catch, minimum biomass, and fishing mortality rate for major groundfish species from 1994 and 1995 logbooks and for the1996 observer data, bottom trawls only.

	1994 logbooks			1995 logbooks			1996 observer data		
Groundfish species	Catch (t)	Minimum stock	Maximum F	Catch (t)	Minimum stock	Maximum F	Catch (t)	Minimum stock	Maximum F
Dogfish	1142	8 279	0.14	711	7 395	0.10	1664	12 446	0.13
Pacific cod	2569	8 702	0.30	1762	5 537	0.32	626	2 743	0.23
Rougheye	1119	5 142	0.22	915	3 379	0.27	1069	6 037	0.18
Perch	4460	26 619	0.17	4936	24 768	0.20	6167	26 626	0.23
Shortraker	482	2 346	0.21	283	865	0.33	144	674	0.21
Silvergray	2170	13 692	0.16	1614	9 165	0.18	1106	6 439	0.17
Yellowtail	893	4 283	0.21	1553	7 776	0.20	1295	4 590	0.28
Canary	783	4 932	0.16	578	4 452	0.13	461	3 246	0.14
Yellowmouth	821	5 982	0.14	979	7 357	0.13	1600	8 048	0.20
Shortspine	651	2 758	0.24	946	3 361	0.28	761	2 085	0.37
Longspine	na	na	na	na	na	0.00	882	840	1.05
Blackcod	378	1 727	0.22	350	1 568	0.22	544	1 946	0.28
Lingcod	2430	8 092	0.30	2007	8 389	0.24	1736	5 211	0.33
Rock sole	1662	5 700	0.29	1580	5 427	0.29	1156	4 471	0.26
Dover sole	2999	10 795	0.28	3358	9 936	0.34	3006	10 872	0.28
English sole	1102	3 517	0.31	1212	3 041	0.40	730	3 261	0.22

particularly well with estimates from the 1996 observer data (Table 3); we cannot tell whether the discrepancies are due to reporting problems with the earlier logbooks, changes in targeting due to price and regulation effects, or changes in availability of some species.

Immediate impacts of effort shifts due to local closures

An interesting policy question that we can address immediately with the results of Table 3 is what the impact on immediate catches of major species would be of closing each of the grounds defined in Fig. 4 as an MPA. Given that effort now occurring on each ground would not just go away, and would instead be redistributed to the remaining grounds, it is not at all clear that closing grounds would cause reductions in catches of all species. In particular, closing a ground that represents a major catch area for a few species could well result in significantly higher total catches of other species on the grounds to which effort would move. Using the attraction weights w_i and profitabilities P_i derived from the gravity model to predict how effort would be redistributed (effort in any remaining area j equal to total effort × w_jP_j/ sum of w_iP_i over the remaining areas), we predict that closing some grounds could cause increases in catches of some species (Table 4), hence implying a need for TAC adjustments following implementation of closed areas (Polacheck 1990).

We can also explore what the immediate effect would be on catches of other species if fishers were required to discard all their catch of each species. For this calculation, we simply set the price of each species to zero and then recalculate profitabilities and predicted efforts for every ground and use these efforts to recalculate all species catches (assuming catch is proportional to effort, so new catch = old catch × (new effort)/(old effort) for every species/ground combination; "old" taken to be 1996 values). Table 5 indicates that such species closures would be largely ineffective even for the target species (total discards nearly as high as the catch now retained). Furthermore, they could have significant adverse impacts on catches of other species due to redistribution of effort into areas where these species are more abundant.

Spatial stock assessment

So far, we have not obtained encouraging results from the simple estimation procedure of searching for species B_0 values that would result in multiples of current FISHMAP estimates of $B_{ij,1996}$. It is easy enough to find B_0 estimates that produce simulated catch sequences that roughly match historical coastwide totals, provided we assume that current biomasses for most species are at least 10 times the FISHMAP minimum estimates in Table 2. For example, Fig. 5 shows a "baseline" simulation with B_0 set so that all species coastwide biomasses end up at 10 times the FISHMAP 1996 estimates for simulation year 1996. However, note in Fig. 5 that the simulated spatial distribution of efforts is quite different from the historical distribution, and the model predicts higher catches in early years than were recorded for many species. The basic problem with both the spatial effort and species catch estimates appears to be that we have not accounted for historical changes in prices and species targeting practices; for example, the model predicts quite high early catches of dogfish and various rockfish species that were not retained until recently. Even when we force the model to match historical spatial effort patterns, catches by ground of some species are grossly overestimated compared with reported landings. It is possible that some of the high catches predicted by the model for years before 1980 did actually occur and were discarded. If so, we need to make a serious effort in future stock assessments to account for the impacts of past discarding, perhaps by using EFFMOD as a tool to reconstruct likely discarding rates. The possibility that dogfish in particular have been discarded at high rates is very encouraging, and even higher impacts might be encouraged in future through modest price supports and bounties.

The single-stock Bayesian assessment procedure (Appendix 2) provides more credible $B_{ij,0}$ estimates for EFFMOD scenario development. Bayes posterior probability profiles

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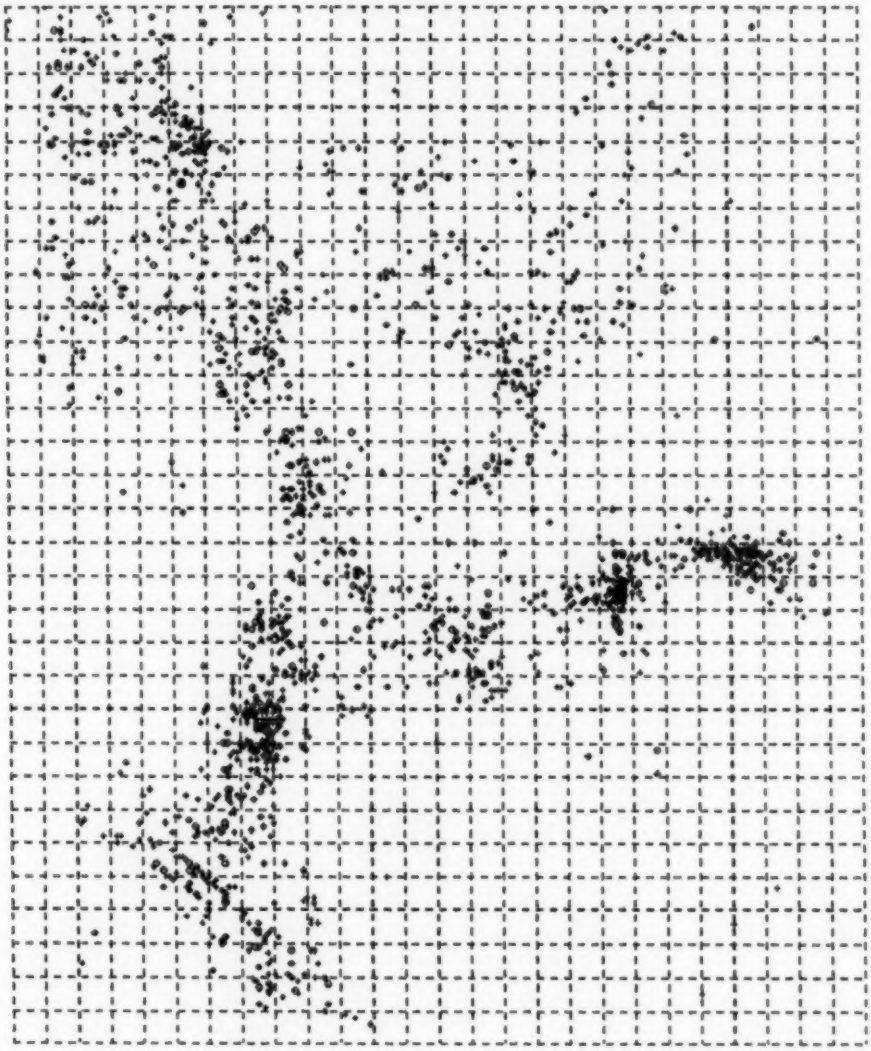
Fig. 3. Locations of trawl set starting points for one heavily fished area in 1996. Each point represents one tow. Grid lines show 1-nmi^2 block boundaries used for spatial assessments; in this assessment, trawling is assumed to sample density randomly within each block. Note that this assumption is violated for some heavily fished blocks.



for $B_{ij,0}$ are presented in Fig. 6, where unfished biomass ranging from $2C_{bar}$ to $200C_{bar}$ (C_{bar} is the 1980–1996 mean reported catch for the stock) is plotted against the relative probability of obtaining the observed 1980–1996 qualified CPUE time series, and trawl survey CPUE time series where available, for corresponding $B_{ij,0}$, assuming qualified CPUE has on average been proportional to biomass since 1980. These profiles show three basic patterns: (*i*) well-determined estimates of $B_{ij,0}$ for some cases where qualified CPUE has dropped dramatically (Fig. 7), generally agreeing fairly well with estimates from other assessment procedures (e.g., POP in Goose Island Gully; Richards and Olsen 1996), (*ii*) monotonic increase in posterior probability with increasing $B_{ij,0}$ for many cases where qualified CPUE has been erratic or shown no temporal trend, which can be interpreted either as lack of historical fishing impact or failure of CPUE to reflect abundance change (increasing q over time due to range collapse, targeting changes, etc.), and (*iii*) monotonic increase in probability, or maximum probability at unrealistically low $B_{ij,0}$, for a few cases like Pacific cod where, luckily, reasonable assessments are available from other methods (Haist and Fournier 1996). Note that some of the qualified CPUE series (Fig. 7) show a few high outliers that could have a large effect on the likelihood calculation of Appendix 2; however, we found that removing these outliers from the assessment did not make much difference to the probability profiles shown in Fig. 6; few of the problem cases show clear trends in qualified CPUE even when outliers are removed from the estimation data.

Using even the optimistic (most probable or upper limit of range tested) $B_{ij,0}$ estimates from the single-stock assessments, EFFMOD predicts that current coastwide trawl catch

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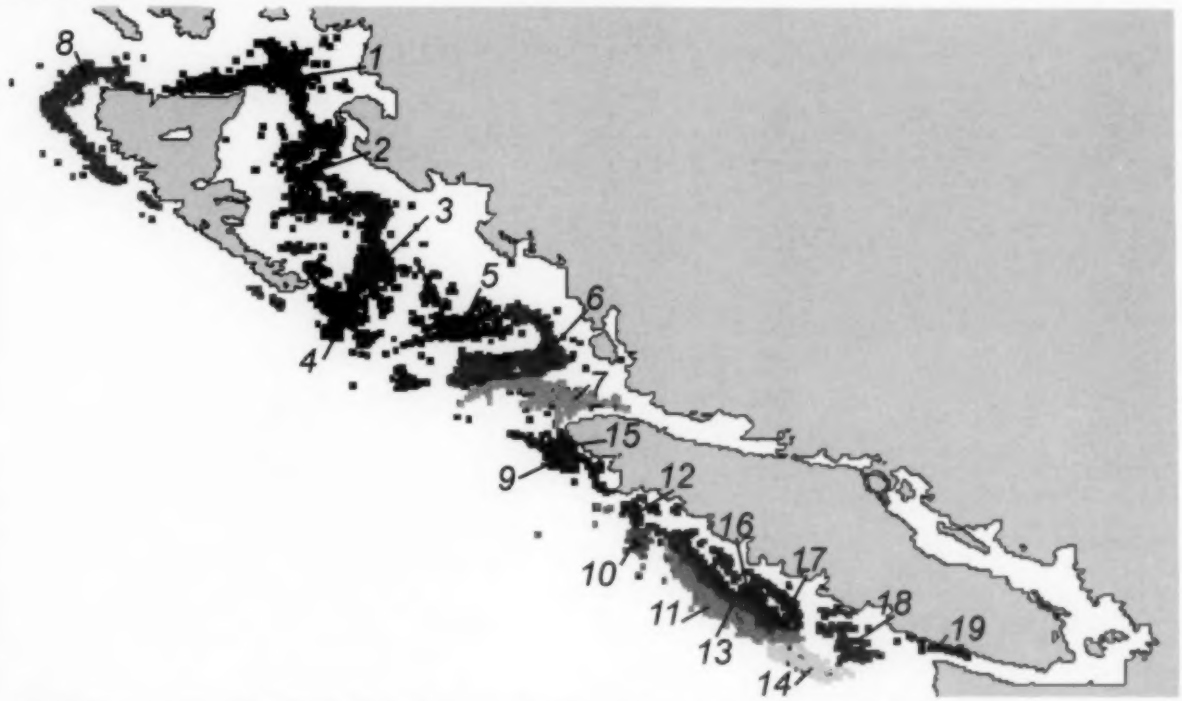
Fig. 4. Major fishing grounds defined from the 1996 observer effort and species CPUE distributions (compare with Figs. 1 and 2). For spatial harvest simulations, each ground is treated as spatially homogeneous with respect to species composition of catch, i.e., fishers are assumed to be unable to target on particular species within each ground.



is unlikely to be sustained, due to declines in some long-lived species. We can only obtain a more optimistic outcome by assuming that unfished biomasses for these species were even larger than the $200C_{bar}$ (C_{bar} is1980–1996 mean landings) used as an upper limit for the Bayes calculations. This rather pessimistic prediction is not so much a consequence of underestimating $B_{ij,0}$ as of the very low estimates of F_{opt} that we obtain for long-lived species under the Beverton–Holt recruitment assumptions described above; as noted earlier, these assumptions generally lead to $F_{opt} < M/2$, i.e., sustainable harvest rates of order 0.02–0.04 for the long-lived species. We consider that it would be dangerously optimistic to assume the sort of strongly compensatory recruitment responses that would be needed to produce much higher F_{opt} estimates, and it certainly appears to us that assuming $B_{ij,0}$ much larger than 200 times recent mean catch would also be dangerously optimistic for most species.

Table 6 presents a disturbing index of current stock status from the single-stock assessment procedure, namely the ratio of current to unfished biomass $B_{ij,1996}/B_{ij,0}$ evaluated at the most likely $B_{ij,0}$ estimator (assuming qualified CPUE proportional to biomass and $B_{ij,0}$ within the range $2C_{bar}$ to $200C_{bar}$, where C_{bar} is mean historical catch for 1980–1996). Values of this ratio <0.5 (about 45% of the cases) indicate probable overfishing, and the instances in Table 6 where the ratio does indicate overfishing mainly involve gross declines since 1980 in qualified CPUE. Such declines are hard to explain by economic effects, although they could arise from movement of fish off some grounds rather than overfishing and from effects of changing trip limits (Richards 1994). Furthermore, we should emphasize that some of the grounds where the model predicts overfishing situations for silvergray rockfish are precisely the grounds that comprise the traditional core of the fishery. Assuming that managers and fishers should not assume the optimistic possibility of movement off of grounds, the most worrisome overfishing cases from our present analysis are POP, shortraker, rougheye (*Sebastes aleutianus*), and canary rockfish, all of which show $B_{ij,1996}/B_{ij,0}$ ratios <0.5 in more than 50% of the grounds (Pacific cod also shows low ratios in most grounds, but it is subject to large recruitment variations).

A matter of obvious concern is whether we have obtained stock size estimates that are too low because of the method used to define fishing grounds and local stocks. Figure 8 compares most probable coastwide biomass estimates from the Appendix 2 procedure for alternative spatial aggregation methods. Happily, we get very similar coastwide estimates no matter whether the stock structure is assumed to be very fine (FISHMAP grounds or minor statistical areas) or coarse (major statistical areas). Of course, local estimates differ; in particular, substocks in the Moresby Gully area cannot be distinguished from substocks in the Goose Island/Mitchell areas using either the minor or major statistical area data. However, biomass estimates obtained using the Appendix 2 procedure and based on our FISHMAP ground partitioning compare relatively well with available estimated biomasses for stocks or statistical areas calculated by the Department of Fisheries and Oceans (DFO) either through surveys or using age-structured analyses (Fig. 9).

Table 7 compares 1997 coastwide quotas with estimates of MSY derived from the estimates of unfished stock size

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Table 3. Estimates of biomass (FISHMAP), effort, profitability (sum of prices × CPUE over species), and attraction weights for the fishing grounds shown in Fig. 4.

	Minimum biomass (t) by fishing ground (grounds in Fig. 5) for 1996								
Groundfish species	1	2	3	4	5	6	7	8	9
Dogfish	1013	1351	252	81	1090	1420	233	114	43
Pacific cod	660	510	76	14	168	141	127	230	19
Rougheye	15	1	62	1064	45	30	10	3724	80
Perch	51	141	1907	6742	3727	2503	987	4109	182
Shortraker	2	0	38	145	11	4	2	302	11
Silvergray	230	289	862	572	737	245	346	1512	207
Yellowtail	140	160	128	41	497	823	615	21	45
Canary	18	77	310	8	285	206	112	43	407
Yellowmouth	3	0	94	902	844	287	1961	756	992
Shortspine	62	4	232	243	24	155	4	621	11
Longspine	4	0	1	15	0	3	0	11	0
Blackcod	175	137	158	107	29	100	120	207	21
Lingcod	163	320	144	81	793	438	273	58	37
Rock sole	573	1654	195	3	407	398	297	17	0
Dover sole	1880	743	715	460	209	1127	146	1670	108
English sole	1318	828	40	15	29	88	106	18	3
1996 effort (h)	3329	3156	2655	3056	1919	3097	3567	2651	737
1996 profitability ($/h)	217	179	184	550	236	231	193	373	343
1996 attraction weight	1.501	1.725	1.413	0.545	0.796	1.317	1.813	0.697	0.211
1995 effort (h)	5913	3530	2282	1575	1400	3343	4434	4060	692
1995 profitability ($/h)	214	163	246	592	171	203	156	317	317
1995 attraction weight	2.474	1.943	0.832	0.238	0.733	1.472	2.550	1.146	0.196
1994 effort (h)	5059	3797	1321	1489	1299	2787	3611	3295	543
1994 profitability ($/h)	205	210	320	457	291	284	139	368	316
1994 attraction weight	2.978	2.180	0.497	0.392	0.538	1.181	3.125	1.079	0.207

using the Appendix 2 procedure. For most long-lived species, this preliminary analysis suggests that current quotas will not be sustainable and that attempts to immediately move to sustainable quotas would result in substantial effort reductions in some areas. The main reason that we obtain lower estimates of MSY than previous DFO assessments is not that our biomass estimates are lower; generally, our estimates are similar to or even higher than those obtained from age-structured assessment methods (Fig. 9). Rather, our estimates of optimum fishing mortality rate and optimum equilibrium stock size (relative to unfished stock size) are substantially lower. A common assessment assumption is the proposal that $F_{opt} = M$ and MSY = $0.5MB_0$. Equilibrium analysis of the delay-difference model, with prudent assumptions about maximum slope of the recruitment curve (five times the recruits/biomass ratio for unfished stock), indicates that optimum stock size is generally around $0.3B_0$ to $0.4B_0$ and F_{opt} is around $0.5M$ to $0.7M$. Hence, our MSY estimates are generally around $0.2MB_0$. Even assuming $F_{opt} = M$, we would conclude high overfishing risk for at least four of the species in Table 7.

Discussion

Effort shifts and MPA design

Our policy simulations demonstrate the critical importance for trawl policy design of predicting changes in spatial distribution of fishing effort (Tables 4 and 5). These results indicate that obvious measures such as MPA's and (or) single-species discarding could very easily do more harm than good by redirecting effort onto alternative grounds. Fishers have warned about this problem for many years, pointing out that regulatory measures used so far in the fishery to protect particular stocks have not reduced fishing impact on the resource as a whole but instead have promoted wasteful discarding and increased impact on other species/grounds. Without a multispecies, multiground model of some sort, it will be practically impossible to see whether the immediate impacts predicted by the model would be dampened or exaggerated by further, long-term shifts in effort distribution.

It is difficult to know how seriously to take the specific impact predictions from the policy simulation results in Tables 4 and 5. These depend on ground attraction weights and profitability estimates that are probably not accurate (and will change in the future), judging from variation among years in estimates of the weights. We can only be confident that effort would be redistributed (e.g., closing a ground would not mean losing the effort that had been directed to that ground entirely; the fishers would still go somewhere) and would impact stocks elsewhere. With the gravity model, we predict that closing a ground would lead to the effort from that ground being widely redistributed over all other grounds; factors not considered explicitly in the gravity model, such as tendencies for fishers to return to the same general areas at the same time of year, might result in the redistributed effort being concentrated more on grounds near the one that was closed. Likewise, fishers may be more or less sensi-

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10	11	12	13	14	15	16	17	18	19
2	156	115	429	1785	171	495	386	567	91
1	13	74	52	11	40	37	87	65	32
4	109	1	101	54	2	4	4	4	0
0	218	7	335	153	28	15	28	1	0
11	49	1	20	26	0	1	1	0	0
1	58	86	191	43	212	25	4	1	0
0	66	73	388	53	54	440	274	63	4
4	147	155	320	151	309	137	54	44	1
0	19	1	125	96	581	8	10	0	0
142	261	13	39	62	2	2	4	1	0
139	501	13	13	70	0	1	7	0	0
59	211	14	81	180	8	13	13	95	0
1	131	131	313	488	120	524	458	180	3
0	4	50	2	3	71	2	13	17	4
113	799	54	408	907	48	53	74	269	69
0	10	12	15	14	14	23	186	48	109
1634	9514	394	2995	1436	663	638	971	257	88
89	88	201	214	258	165	189	97	94	
1.793	10.633	0.192	1.372	0.547	0.394	0.331	0.980	0.266	
264	4152	618	2751	1923	1842	749	1699	362	149
110	146	148	164	242	99	104	108	49	93
0.215	2.552	0.374	1.503	0.711	1.662	0.646	1.409	0.660	0.143
6	2547	300	2956	2342	1721	1662	1548	484	341
354	171	202	174	207	167	83	179	70	150
0.002	1.792	0.179	2.049	1.365	1.243	2.421	1.042	0.827	0.275

tive in their fishing site choices to loss of opportunity to take particular species than we predict just on the basis of impact on comparative profitability of alternative fishing grounds. The only way to really test the detailed gravity model predictions would be to close some ground (or species) to fishing and then observe how effort is actually redistributed; such tests may happen if MPA's are developed for the B.C. coast. Until such tests are conducted, we recommend using the effort distribution "submodel" only for broad assessment of coastwide impact of regulatory measures that may substantially alter the spatial distribution of trawling opportunities, not for predictions of impact on any specific fishing ground or species.

Insights into the B.C. groundfish fishery

Comparison of FISHMAP spatial analyses with DFO assessments (Haist and Fournier 1996; Richards and Olsen 1996; Saunders et al. 1996; Stanley 1996; Fargo and Kronlund 1997) suggests strongly that only small proportions of most stocks are vulnerable to fishing at any moment, i.e., the vulnerability factors (1 + (unfishable biomass)/(fishable biomass)) are mainly quite large. However, this finding does not in any way imply that the stocks are safe from overfishing or that the stability of the fishery is insured by the existence of "natural" MPA's. To the contrary, the 1996 observer data indicate that there must be relatively rapid exchange of animals between fished and unfished areas, or we would have been able to detect local depletions in times/areas of intense fishing. Rapid exchange implies in turn that there is no effective protection of most stocks due to fishing being restricted to a few sites. If some aspect of the fish–fisher interaction has helped to stabilize or protect the biodiversity of the system, that aspect is much more likely to be the large-scale redistribution of fishing effort among grounds in response to changes in local profitability of fishing.

Review of DFO assessment documents indicates that roughly 50–65% of the current (1996–1997) landed value of groundfish (excluding Pacific hake (*Merluccius productus*)) is from species/stocks for which reasonable estimates of current abundance are not available from age- or size-structured assessment methods. That is, at least half the current landed value is from stocks for which we lack accurate estimates of current biomass, and for most of these stocks, we would have trouble even defending trend assessments based on CPUE or catch histories. This observation is not a criticism of DFO groundfish scientists; they have done a remarkable job considering limited resources for data gathering and analysis. Rather, it reflects the outrageous ecological complexity of the B.C. groundfish resource. Further, it is unlikely that this state of affairs will change much in the next few years. There are not going to be a lot more groundfish scientists, and even if there were, it would be impossible to reach back in history to collect the detailed data needed for age-structured assessments. Further, there is little hope that we will be able to successfully extrapolate results from the few elaborate assessments (like POP in Goose Island Gulley) even to other stocks of the same species, let alone to the variety of species for which little data have been gathered (there is no reason

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Table 4. Predictions of short-term change in annual catches by ground due to closing each of the grounds shown in Fig. 4.

Ground closed (Fig. 5)	Dogfish	Pacific cod	Rougheye	Perch	Shortraker	Silvergray	Yellowtail	Canary	Yellowmouth
1	–181.3	–202.1	88.5	459.6	11.4	67.1	50.2	26.2	109.6
2	–110.6	–115.2	83.6	423.9	11.1	40.6	67.0	21.5	103.6
3	51.5	32.0	42.7	–161.8	–4.4	–83.1	57.5	–20.1	70.3
4	93.2	42.2	–155.7	–2578.2	–31.8	–0.9	82.6	31.9	–356.9
5	–55.6	6.0	44.7	–52.6	5.3	–5.8	–50.4	–7.2	17.9
6	–37.6	12.5	73.3	–131.2	10.2	21.8	–151.6	–3.6	57.8
7	62.6	–20.4	93.5	239.0	12.1	–148.3	–213.9	10.9	–158.5
8	81.6	28.3	–556.1	–308.5	–30.8	–147.8	71.0	21.2	–51.4
9	12.1	4.4	–17.2	–25.2	–2.7	–19.0	12.0	–34.2	–225.4
10	59.5	23.6	41.5	218.2	4.1	39.8	45.8	17.2	51.7
11	379.5	165.5	180.5	1368.2	10.3	277.3	316.8	97.3	361.8
12	–15.4	–3.8	9.7	48.3	1.2	–16.5	–10.3	–27.9	11.9
13	–89.2	28.7	17.8	204.6	1.5	–0.2	–224.3	–64.8	2.2
14	–98.1	19.0	18.7	157.6	–4.5	31.2	33.5	–11.2	12.7
15	–2.9	–6.6	16.4	84.9	2.2	–53.5	4.7	–24.3	–2.0
16	–57.5	4.2	15.8	82.5	2.0	12.7	–54.3	–13.8	18.3
17	–6.1	6.9	23.7	126.0	3.2	23.1	6.1	1.3	29.8
18	–11.1	–1.6	6.1	33.1	0.8	5.9	4.5	1.1	7.8
19	–6.0	–1.2	2.2	11.3	0.3	2.0	1.8	0.9	2.7

Note: Prediction are based on shifting effort from the closed ground to all other grounds in proportion to the profitabilities and attraction weights of Table 1 using the effort distribution model defined in the text.

to expect spatial consistency or similarity among stocks in the vulnerability factors that make q_{ij} highly uncertain and prevent accurate expansion of spatial analyses like FISHMAP CPUE maps or DFO surveys).

If observer programs are continued, thus providing detailed and reliable information on the spatial distribution of fishing and catches, spatial analysis systems like FISHMAP should eventually (after a decade or two) allow us to make much better assessments of trends in abundance and stock structure than is possible today with only crude historical catch and effort statistics. But this is little comfort to those who fear that the current fishery is already eroding stock structure, especially of long-lived species that would take decades or more to recover. Historical catch statistics do not indicate that this fear is warranted, but those statistics may be badly corrupted by misreporting and discarding that in turn have been partly due to well-intentioned regulatory measures (Richards 1994).

Management implications and alternative regimes

How should the fishery be managed today, given (*i*) extreme uncertainty about many stock sizes and the likelihood that this uncertainty will persist for at least the next two decades, (*ii*) a good chance that most obvious regulatory measures like MPA's and species quotas will have unintended side effects due to their impacts on effort distributions, discarding, and information gathering, and (*iii*) growing public concern about impacts of the fishery, especially on long-lived species? The best answer to this question is very likely not to be found in either shutting down the fishery, as some environmentalists have suggested, or in simplistic regulatory measures like combined species quotas. Output control or quota management is dangerous and costly in settings where it is not economical to measure stock sizes accurately over time (see discussions in Walters and Parma (1996) and Walters and Pearse (1996)). Further, combined quotas cannot protect biodiversity (since such quotas depend mainly on the more abundant species and hence will not respond adequately to depletion of rarer species) and could cause large-scale effort redistribution with more damaging effects than the current distribution. Obviously, these comments have implications for the IVQ system introduced into the fishery in 1997; in view of current uncertainties about stock sizes, we see no way to set IVQ's without either placing some species/stocks at considerable risk (set quotas near or above recent catches) or foregoing considerable income to fishers (set quotas much lower than at present).

Simulations of species/ground quota management (set TAC or quota for each species on each fishing ground), with or without ground closure when any species quota is filled, indicate that these strategies could succeed in maintaining spatial and species diversity of the fishery provided the quotas are adjusted annually on the basis of accurate stock size estimates. Even if inaccurate estimates are used to set the quotas, spatial effort redistribution processes should help to prevent some of the worst depensatory effects that overestimation of safe local quotas would otherwise have (fishers should tend to exert less effort in areas that have been locally depleted, whether or not this depletion has been seen by the stock assessment process). Without the closure-on-quota option, there could be substantial discarding, but there would be minimal redistribution of fishing effort and hence unintended side effects on other stocks. With local closure upon reaching the first species quota, discarding would be avoided, but there would be more substantial (and hence risky) effort redistribution along with considerable cost for enforcing the closures. So far, the simulations have not indicated any substantial advantage of ground-scale "micromanagement" over the much simpler strategy of limiting effort and counting on spatial effort redistribution processes to prevent localized overfishing.

In view of our concerns about ability to set safe IVQ's for

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Shortspine	Longspine	Blackcod	Lingcod	Rock sole	Dover sole	English sole
48.3	70.5	3.0	77.8	–47.6	–374.4	–450.8
56.1	66.9	21.9	–2.7	–516.9	105.4	–71.5
–23.4	55.1	–11.1	91.6	37.2	3.6	41.9
–11.0	61.3	8.6	102.9	77.1	93.7	52.6
31.3	39.4	20.0	–174.7	–57.4	101.8	27.8
7.3	64.3	13.8	–2.1	–19.4	–118.1	32.3
64.6	76.3	5.5	–66.1	–13.0	229.9	33.3
–76.4	53.8	–11.0	93.4	65.8	–208.7	45.1
7.7	14.6	–3.4	17.9	17.6	1.7	12.1
–63.2	–121.0	–6.7	61.0	40.0	72.5	28.0
–147.9	–582.2	–42.5	356.6	287.7	309.0	198.8
5.9	6.3	2.6	–22.8	2.0	10.6	3.4
35.2	58.7	–2.6	–170.3	75.0	17.0	45.6
–1.9	–10.1	–26.5	–103.8	34.9	–324.2	23.3
11.0	13.2	6.3	–25.9	11.7	34.4	8.1
10.7	12.4	6.3	–86.6	15.1	36.4	8.4
16.2	18.8	10.9	–71.2	21.2	60.6	–6.9
4.2	5.1	–3.0	–3.8	5.1	–0.7	0.2
1.5	1.7	1.0	3.0	2.0	1.4	–6.9

many species/grounds, we wonder if the best management strategy might not be to simply (*i*) limit total coastwide effort by giving each license holder a transferable "effort quota" denominated as an annual swept area (fishing time × speed × trawl width), (*ii*) eliminate all area-specific effort and catch restrictions except for a few very carefully selected MPA's aimed at protecting key areas of high biological diversity and (or) bycatch of Pacific halibut (*Hippoglossus stenolepis*) and sablefish (blackcod) (*Anoplopoma fimbria*), and (*iii*) maintain a threat of permanent closures in areas where there are dense, single-species aggregations of rockfish, should fishers choose to target such areas and should FISHMAP methods reveal rapid local depletion of the aggregations. This system is in fact not far from how the fishery operated before IVQ's and would at least insure the best possible economic environment for gathering good information to reduce uncertainty as rapidly as possible short of massive fishery-independent surveys. It would rely upon changes in profitability of grounds that start to become overfished to shift effort away from such grounds. If it were accompanied by a large program to tag Pacific halibut and sablefish discards, we might even be able to show that survival of these discards is so low that it would be better to retain them and use proceeds from their sale to help cover research/monitoring costs for all the demersal fisheries. Further, it would at least be a conservative system, with no pretense that there is some way to achieve the IVQ recommendations from single-species assessments without causing substantial risk of local stock collapses.

An important conservation concern about the effort limitation strategy is that fishers may elect to target on dense and highly vulnerable aggregations of some rockfish species (shortraker, silvergray, yellowtail (*Sebastes flavidus*), canary, and yellowmouth (*Sebastes reedi*); see Fig. 1) and deplete these much more rapidly than we would predict from ground-scale effort redistribution based on combined species profitability. The IVQ system prevents fishers from doing this by creating a threat of protective closures should any species/area quota be exceeded. Probably the best way to address this issue with minimum disruption to fishers is to continue the detailed logbook program based on independent observers and use FISHMAP or other spatial statistics methods to closely monitor interannual changes in the aggregation patterns of worrisome species. Resulting data should demonstrate whether pathological targeting does occur and should allow development (and enforcement) of precisely located (and minimally disruptive) MPA's for the aggregations. Indeed, it may be cheaper for fishers to pay for the observer program on a permanent basis than to incur substantial losses in fishing opportunity due to the much larger closures that will now occur if area quotas are exceeded.

Uncertainty and recommendations for improved assessment

A key reason for trying to fit the overall multispecies model directly rather than just driving it with single-species assessment results is that we could then account to at least some extent for effects of dispersal/migration between fishing grounds. However, the model is extremely sensitive to low mixing rates between areas, at least for long-lived species, under policy scenarios and harvesting regimes that involve local closures (MPA's) combined with large-scale depletion. This sensitivity is perhaps obvious in hindsight. Consider, for example, the problem of predicting stock size recovery for long-lived species in a single-ground MPA intended to protect these species. Population growth rates in such an MPA are likely to be in the order of 5%/year. If dispersal rates out of the MPA are just 5% as well, and if these emigration losses are not balanced by immigration from surrounding depleted areas, the model predicts that stocks in the MPA will fail to recover. Considering the data available for model fitting, it is unreasonable to expect that any as-

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Table 5. Predictions of short-term change in annual catches by species, due to forcing complete discarding of each other species (we set the price of species in each row to zero and then calculate effect on spatial effort distribution and hence catch of species listed across the columns).

Groundfish species discarded	Predicted immediate change (t) (from 1996 base) in catches of other species								
	Dogfish	Pacific cod	Rougheye	Perch	Shortraker	Silvergray	Yellowtail	Canary	Yellowmouth
Dogfish	–27.2	–10.6	17.2	73.2	1.8	5.6	–9.5	–3.5	14.9
Pacific cod	–47.1	–47.8	34.3	158.7	4.6	5.2	0.6	2.7	26.4
Rougheye	40.6	20.4	–154.7	–176.3	–10.3	–31.7	31.1	6.3	–33.2
Perch	120.7	80.7	–212.4	–2185.6	–30.4	–90.9	8.1	9.6	–300.4
Shortraker	4.6	2.9	–6.9	–13.5	–0.7	–0.3	4.4	0.6	–1.5
Silvergray	9.4	–0.0	–20.9	–8.8	–0.5	–63.0	–30.2	–15.3	–31.1
Yellowtail	–42.9	–0.6	51.1	136.4	6.3	–23.1	–126.3	–20.9	–6.0
Canary	–13.7	2.5	14.2	59.8	1.1	–11.4	–19.1	–16.2	–5.1
Yellowmouth	18.9	8.3	–32.9	–245.4	–3.9	–43.3	–30.9	–15.5	–159.8
Shortspine	109.3	51.7	13.4	281.0	0.4	56.8	91.3	26.1	92.8
Longspine	129.6	58.6	70.8	493.5	4.6	97.9	111.4	34.4	126.5
Blackcod	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lingcod	–104.1	0.6	93.9	374.4	9.9	5.4	–109.9	–33.4	48.8
Rock sole	–67.7	–66.9	61.7	230.9	7.9	11.3	7.5	9.3	53.4
Dover sole	–53.4	–23.2	17.4	443.7	1.2	61.4	66.9	11.0	117.6
English sole	–61.0	–62.2	-37.1	181.2	4.8	21.5	14.0	8.2	41.0

Note: Making a species unprofitable to retain generally reduces its catch somewhat (and none would be landed), but in many cases would cause increase in catch of other species due to spatial shifts in fishing effort).

sessment model will allow us to estimate dispersal rates by comparing model fits with and without these rates. If MPA's are to be a major policy option, there will need to be substantial tagging programs to directly measure dispersal losses from such MPA's.

Our analysis clearly shows the importance of information for dealing with stock size uncertainties in the fishery. Bayes posterior probability plots for $B_{ij,0}$ estimations using qualified CPUE and recruitment anomaly information as the only stock trend data source compare poorly with corresponding plots derived from analyses that also incorporate survey data (Fig. 10).

EFFMOD simulations of historical catch starting with the single-stock $B_{ij,0}$ estimates derived with the Appendix 2 procedure suffer from the same problem of overpredicting catches of some species (that were discarded until recently) as we noted above for the whole-model fitting procedure (Fig. 11). Further, to match recent catches at all closely, we had to use the single-species q_{ij} estimates from the Appendix 2 eq. A12 method; the estimates based on qualified CPUE alone are generally about twice as high; this is not surprising considering that the qualified efforts used in the fits are often half or less of the total effort "supplied" to each ground each year in the EFFMOD multispecies simulations. As measured by the Shannon–Weiner effort diversity index D_e, EFFMOD distributes effort more evenly for past years than is evident in the historical data while predicting no strong trends in the species diversity indices D_j. It is clear that the next priority for further development of EFFMOD will have to be inclusion of historical price and discarding information for each species, at least as a yes/no time series representing when fishers started retaining the species.

There are two huge uncertainties about the future of the fishery under any management strategy, and unfortunately, neither of these is likely to be resolved if research continues to be preoccupied with traditional assessment issues like recruitment variation. First, we do not know the current exploitation rate on many long-lived species, so we cannot even say whether relative stability in historical catches is due to conservative management or slow mining of accumulated biomass. Second, and even more important, we do not know whether the current grounds represent special attraction sites for some species, such that dispersal/mixing rates out of these sites are density dependent. If the mixing rates are not density dependent, then densities on the grounds will vary in proportion to densities outside the grounds, and spatial CPUE mapping of densities on the grounds will provide an index of stock trend that can be used on decadal time scales to detect whether some long-lived species are being overfished. But if emigration rates from the grounds are positively density dependent (e.g., m'_{ij} in Appendix 1 varies as kD_{ij}), then density on the grounds will vary as a low power (<<1.0, 0.5 if $m' = kD$) of total stock biomass (as occurred in the Newfoundland northern Atlantic cod (*Gadus morhua*) decline; see Hutchings and Myers 1994), and CPUE will remain high until the unfished "reserve" has been severely depleted. In short, density dependence in emigration rates implies that we would be unable to "see" stock trends through analysis of CPUE data.

Unfortunately, there does not appear to be any practical and relatively inexpensive way to resolve the uncertainty about density-dependent movement and erosion of unfished reserve abundance. Tagging studies can be used to measure mixing rates and spatial scales of mixing, but such studies are unlikely to reveal whether the rates are density dependent unless they are carried out for many years under widely contrasting density "treatments" created by experimental depletion fishing. Direct measurement of trends in abundance in unfished areas would require fishery-independent surveys, both off the bottom and in areas "near" fishing grounds, using methods other than trawling; further, these surveys would have to be carried out on decadal time scales to detect

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Shortspine	Longspine	Blackcod	Lingcod	Rock sole	Dover sole	English sole
9.3	12.6	1.6	–22.6	–16.9	–14.9	–17.1
21.7	30.0	5.1	–3.3	–73.3	–29.2	–77.3
–26.7	–1.4	–5.4	40.7	41.2	–45.0	29.0
–24.7	112.7	5.2	91.7	109.7	57.1	130.7
–2.6	–3.2	–0.8	4.5	5.4	–2.1	3.9
9.0	38.6	2.4	–14.1	1.6	29.7	18.5
32.1	50.0	8.0	–99.4	4.0	52.4	14.5
7.3	11.3	1.2	–28.3	8.5	8.1	9.1
11.7	34.2	–0.0	–7.7	23.4	29.5	26.1
–67.2	–158.6	–14.4	112.7	91.0	55.6	62.3
–70.9	–220.2	–16.3	123.1	101.7	105.7	70.3
0.0	0.0	0.0	0.0	0.0	0.0	0.0
53.2	57.8	14.2	–220.9	–17.1	62.7	19.5
37.0	50.6	13.3	–17.8	–243.1	38.8	–58.9
–19.0	–47.5	–20.4	45.0	42.6	–278.0	–87.0
21.4	29.6	4.4	10.4	–52.1	–78.4	–125.5

Fig. 5. Baseline simulation results from the EFFMOD multispecies, multiground delay-difference model, with historical efforts simulated by the gravity model and unfished biomasses set for each species at a coastwide value that results in the 1996 biomass being 10 times the FISHMAP minimum estimates in Table 2. Upper panels show historical data and lower panels are simulated data. Note that historical catches are overestimated in early years mainly due to failure to include discarding of some species in the simulations. Efforts are shown as cumulative over grounds, with the lowest line representing ground 1 in Fig. 5. Catches are also shown as cumulative over species, with dogfish on the bottom and other species added in order of appearance in Tables 1–5.

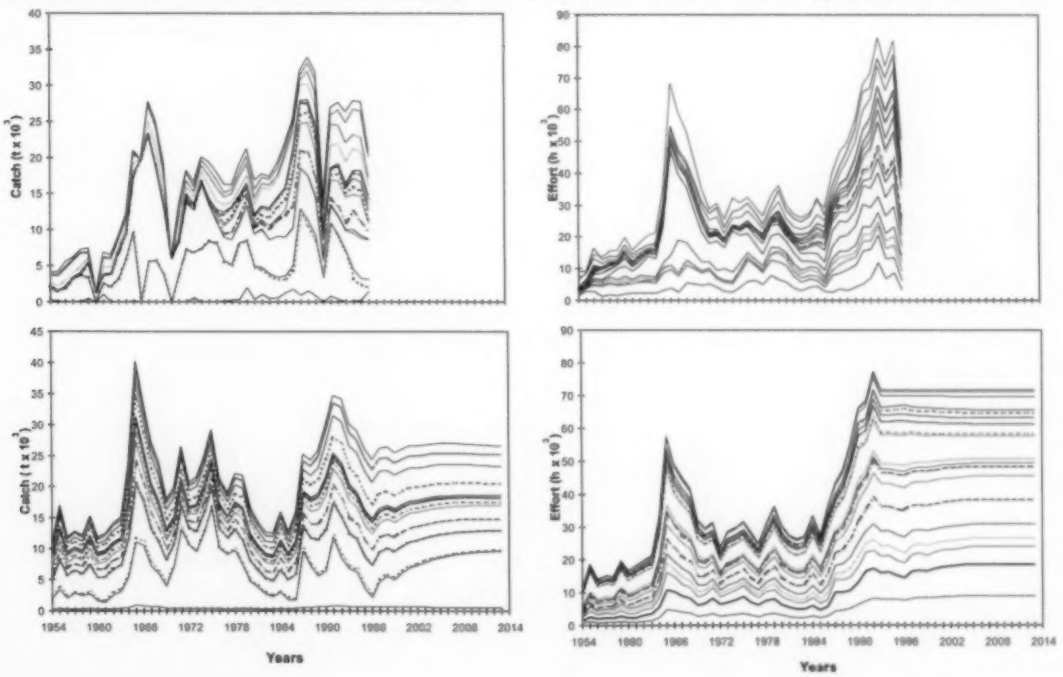

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Fig. 6. Bayes posterior probability profiles for $B_{ij,0}$ using the assessment procedure in Appendix 2. The x-axis of each plot is unfished biomass, ranging from $2C_{bar}$ to $200C_{bar}$ where C_{bar} is the 1980–1996 mean reported catch for the stock. The y-axis of each plot is the relative probability of obtaining the observed 1980–1996 qualified CPUE time series for corresponding $B_{ij,0}$, assuming that qualified CPUE has on average been proportional to biomass since 1980.

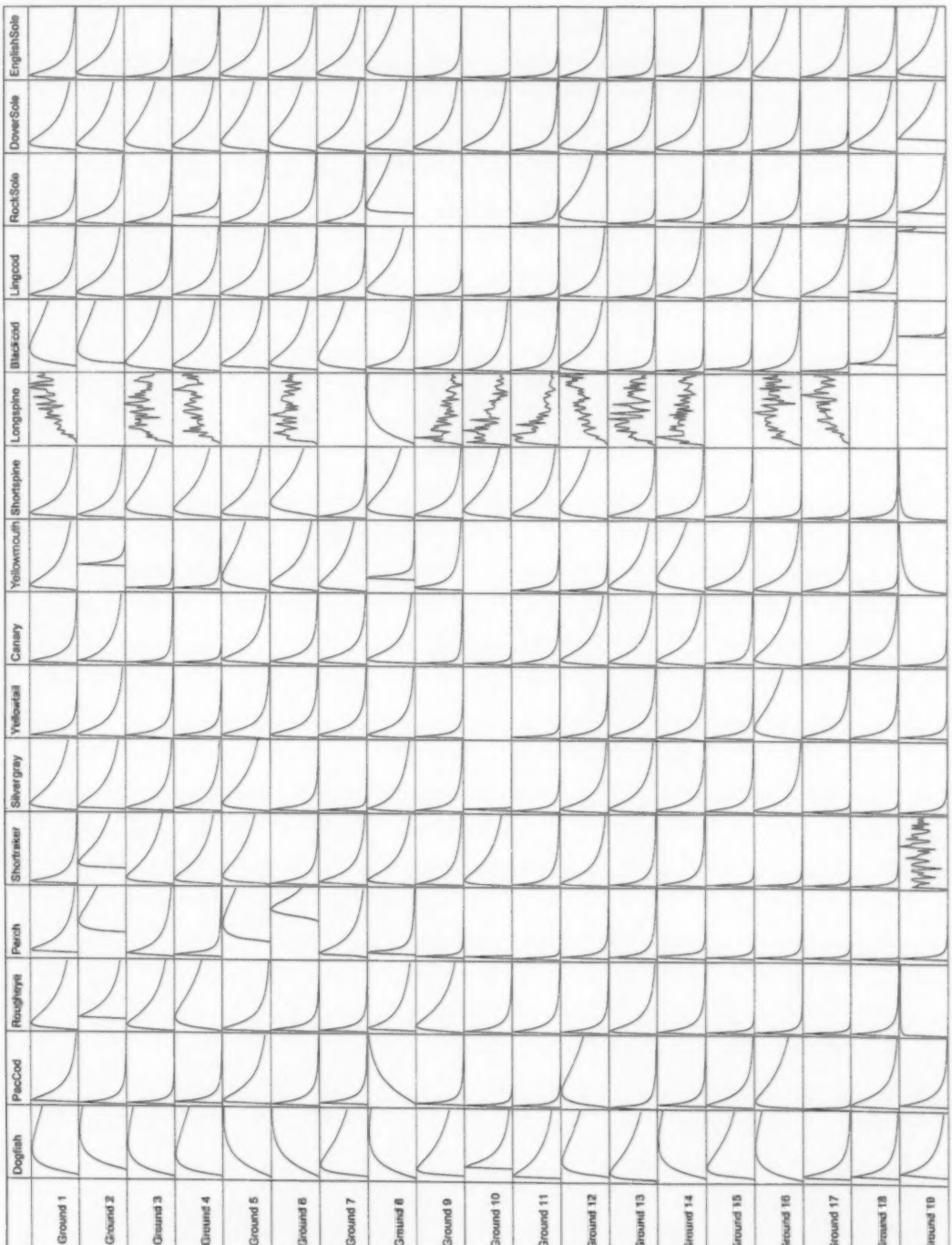

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Fig. 7. Comparison of observed 1980–1996 trends in qualified CPUE (small circles) with CPUE predicted (solid line) from most probable unfished biomass $B_{ij,0}$ estimates in Fig. 7. For each plot, predicted CPUE represents the most probable trend in biomass for the stock, rescaled to the same units as qualified CPUE by using the maximum likelihood estimate of catchability q_{ij} for qualified effort. Larger circles represent survey data.

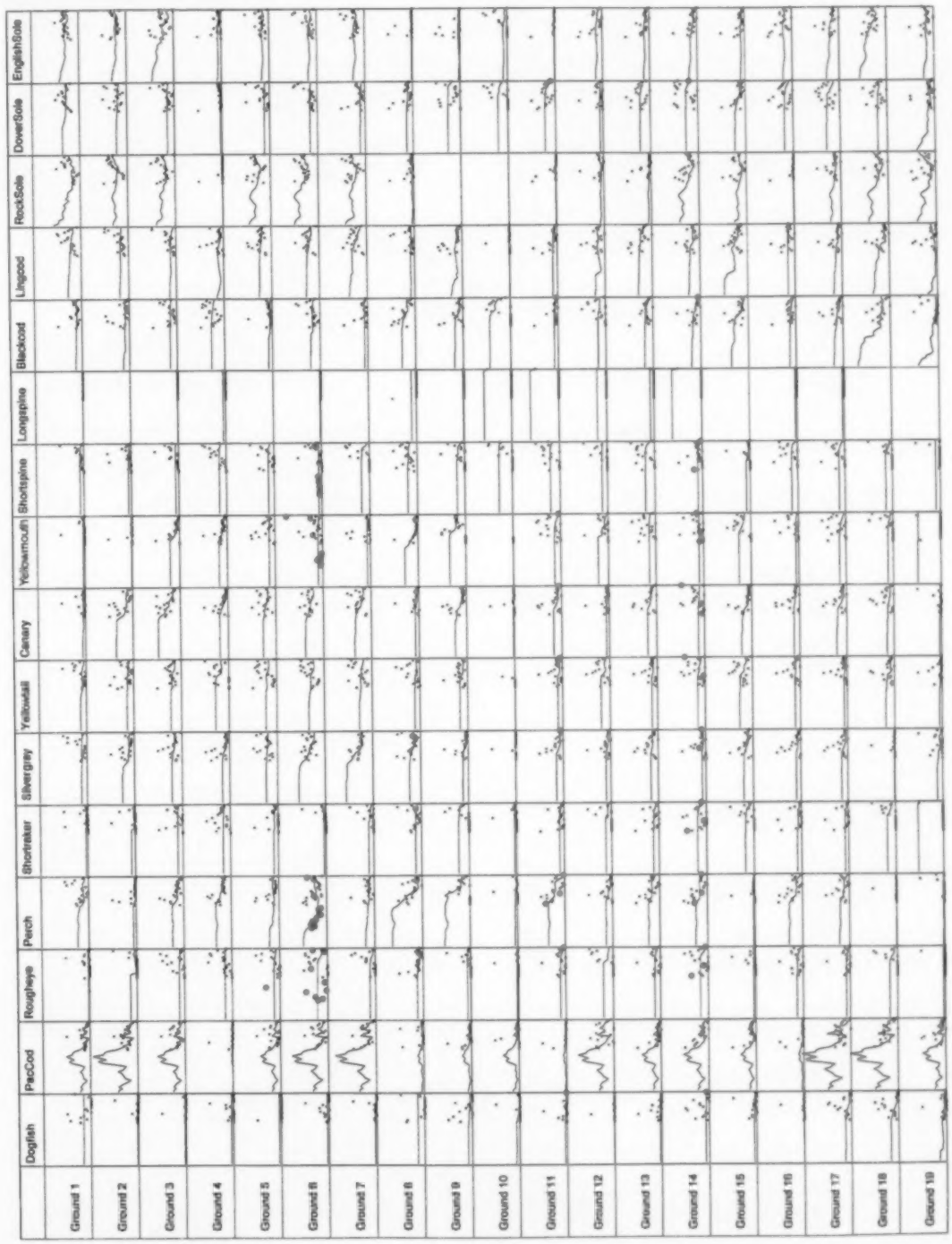

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Table 6. Species/ground estimates of the stock status ratio $B_{ij,1996}/B_{ij,0}$ based on unfished biomass $B_{ij,0}$ from the single-species assessment procedure in Appendix 2.

	FISHMAP ground																		
Groundfish species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Dogfish	0.89	0.84	0.92	0.85	0.96	0.96	0.72	0.95	0.51	0.21	0.37	0.70	0.72	0.88	0.70	0.93	0.38	0.26	0.21
Pacific cod	0.17	0.16	0.17	0.19	0.21	0.15	0.18	0.26	0.18	0.11	0.15	0.24	0.01	0.19	0.19	0.22	0.04	0.18	0.19
Rougheye	0.74	0.32	0.72	0.86	0.59	0.38	0.40	0.51	0.72	0.41	0.37	0.44	0.57	0.38	0.33	0.35	0.39	0.42	0.97
Perch	0.37	0.48	0.33	0.32	0.60	0.51	0.45	0.12	0.28	0.15	0.03	0.25	0.30	0.40	0.30	0.12	0.21	0.03	0.13
Shortraker	0.41	0.42	0.74	0.71	0.72	0.37	0.40	0.70	0.32	0.73	0.35	0.57	0.33	0.36	0.36	0.22	0.36	0.43	0.95
Silvergray	0.83	0.43	0.66	0.60	0.81	0.44	0.37	0.61	0.47	0.68	0.49	0.67	0.73	0.68	0.48	0.66	0.53	0.60	0.34
Yellowtail	0.48	0.67	0.60	0.59	0.75	0.72	0.66	0.63	0.51	0.91	0.52	0.48	0.66	0.57	0.54	0.88	0.68	0.29	0.55
Canary	0.41	0.31	0.32	0.39	0.65	0.59	0.51	0.65	0.29	0.41	0.35	0.67	0.54	0.77	0.40	0.77	0.34	0.60	0.30
Yellowmouth	0.64	0.26	0.16	0.31	0.85	0.77	0.69	0.21	0.44	1.00	0.34	0.14	0.71	0.86	0.55	0.53	0.28	0.36	0.96
Shortspine	0.60	0.51	0.82	0.79	0.71	0.87	0.31	0.79	0.47	0.79	0.65	0.83	0.54	0.33	0.18	0.33	0.34	0.37	0.97
Longspine																			
Blackcod	0.80	0.74	0.80	0.75	0.53	0.68	0.82	0.54	0.29	0.41	0.39	0.72	0.38	0.27	0.24	0.39	0.23	0.29	0.12
Lingcod	0.62	0.79	0.48	0.50	0.72	0.63	0.39	0.83	0.50	0.52	0.49	0.53	0.45	0.50	0.26	0.86	0.43	0.40	0.60
Rock sole	0.39	1.01	0.72	1.10	0.69	0.72	0.70	1.16	0.48	1.00	0.69	1.14	0.79	0.73	0.63	0.81	0.71	0.75	0.85
Dover sole	0.73	0.76	0.83	0.76	0.81	0.86	0.66	0.60	0.67	0.64	0.45	0.78	0.63	0.72	0.19	0.46	0.48	0.78	0.38
English sole	0.72	0.88	0.37	0.53	0.88	0.82	0.87	0.99	0.44	0.66	0.66	0.61	0.64	0.58	0.64	0.94	0.51	0.58	0.89

Note: Values <0.5 of the status ratio indicate that the stock is currently overfished (shaded). Improved "filtering" of qualified CPUE to exclude years before species were retained, and high outliers, would increase the proportion of stocks in the high-risk category.

Fig. 8. Comparability of coastwide biomass estimates based on alternative spatial aggregation methods. Each point represents one species.

Fig. 9. Comparison of available DFO terminal biomass estimates and Appendix 2 procedure biomass estimates based on fishing grounds. Each point represents a species/stock or species/statistical area.

differential decline in unfished areas. A key weakness in the survey approach, even if an economical survey method were available, is that we do not know how to define "near", especially considering that some species likely exhibit complex seasonal movement patterns that may be linked to simpler behaviors that cause localized spatial mixing.

Both uncertainties could be resolved at once if we could develop a reliable, relatively inexpensive method for in situ, permanent tagging of fish over wide areas. Exploitation rates (and spatial variation in these rates) could then be measured directly from tag recovery rates, without concern about mortality due to handling and tagging, and we could accumulate information on density-related changes in movement pat-

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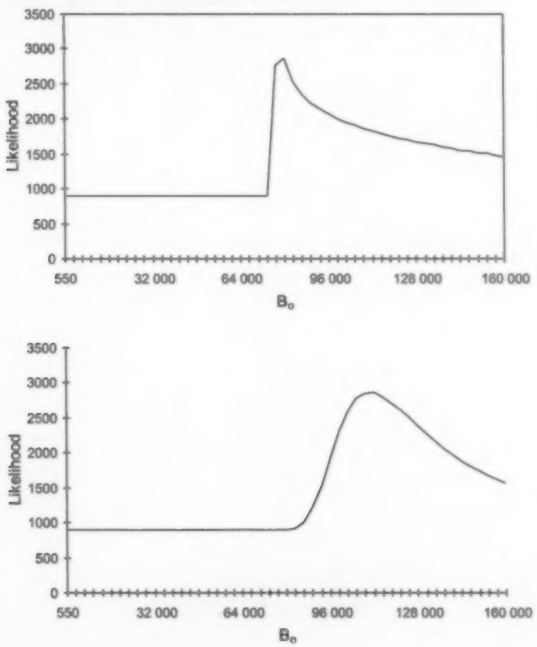
Table 7. Comparison of current catches and fishing quotas against estimates of minimum (0.2 rule) and most probable MSY levels by species (t).

Groundfish species	1994–1995 average catch	1991–1996 average catch	1997 quota	Minimum estimate MSY	Most probable MSY	Significant overfishing risk
Dogfish	182	258	5440	239	502	?
Pacific cod	2585	5046	2574	7870	8238	Variable
Rougheye	1104	550	380	180	263	Yes
Perch	5342	3106	6481	2767	3283	Yes
Shortraker	398	158	77	32	49	Yes
Silvergray	2199	1235	1510	949	1226	Yes
Yellowtail	3020	2622	5233	1622	2188	Yes
Canary	905	689	929	416	542	Yes
Yellowmouth	1150	766	2430	345	463	Yes
Shortspine	907	377	748	96	184	Yes
Longspine	na	na	860	40	110	?
Lingcod	2899	2434	2887	1760	2157	
Rock sole	1871	1985	2082	1391	1679	
Dover sole	3622	2257	3073	1228	2102	Yes
English sole	1196	983	791	681	1003	

Fig. 10. Comparison of initial biomass (B_0) estimates for POP in Goose Island Gully using the Appendix 2 procedure. Note the improvement in the posterior probability distribution of biomass estimates when survey information is considered in the estimation (lower panel) in addition to the CPUE and recruitment anomaly data (upper panel).



terns. For instance, there is a proposal in Australia to try in situ tagging using feeding stations with chemical and radiotracer feeds and an inexpensive video apparatus to record species/size information on each consumption event of labelled food.

If the financial burden for groundfish research and stock assessment continues to shift onto the industry, the issue of whether to invest in survey or tagging programs will become a key matter for debate. To the extent that every vessel in the trawl fleet will bear a share of the financial burden, there is incentive for every one of them to help reduce research costs by contributing at least some time to acting as a research platform operating at relatively low marginal cost given that they are already at sea much of the time. We need to develop scientific consensus on how they should spend that time, e.g., running acoustic transects across fished through unfished areas or deploying/servicing in situ tagging stations. Further, we need to make it absolutely clear that we are not going to pull any magical assessment rabbits out of our hats just by finding better ways to analyze the commercial catch and effort statistics.

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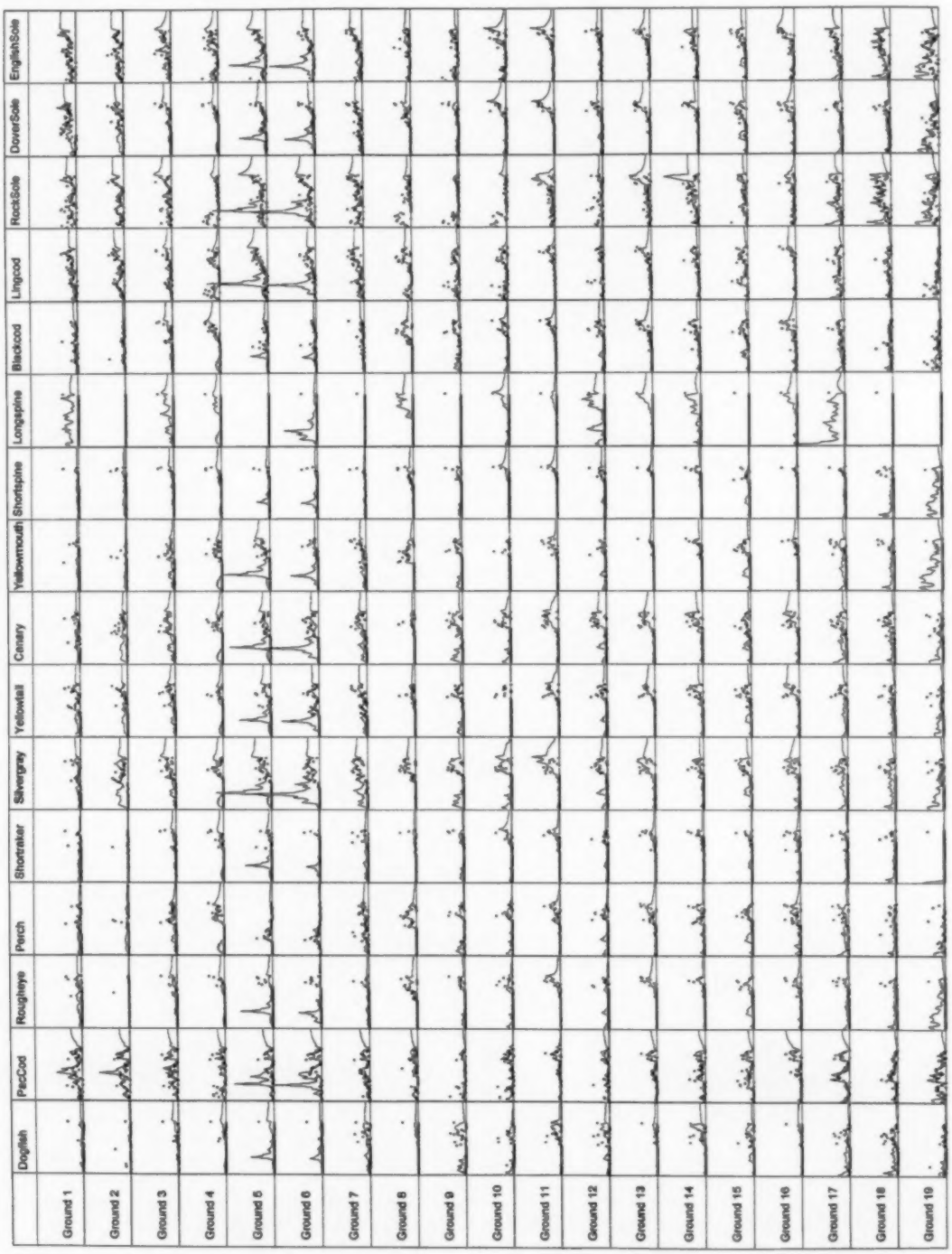
Fig. 11. Predicted catches for 1954–1996 by species and ground from the EFFMOD simulator compared with reported catches. For this scenario, EFFMOD efforts were set to historical values for each ground, and biomasses were set initially at $B_{ij,0}$ most probable values from the single-stock assessment procedure.



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Appendix 1. Derivation of the gravity model for spatial effort allocation from considerations of local fish availability and effort movement

The low biomass density estimates from FISHMAP for most grounds compared with catches suggest that fish are mixing relatively rapidly between these grounds and areas/depths where trawling is either physically impossible or unprofitable, such that the biomass present at any moment on a ground is generally only a small proportion of the biomass that contributes to catch over annual time scales. This means that local catch rates and profitability may be quite sensitive to (or may at least be perceived by fishers to be sensitive to) local effort density on each ground. Further, fishers can redistribute effort rapidly among fishing grounds in response to changing profitabilities. The gravity model (eqs. 3 and 4) can be derived by combining these observations in two steps: (*i*) we derive a model for short-term (day–week–month time scale) equilibrium biomass density available on each ground as a function of mixing rates and effort density and (*ii*) assuming that profitability is levelled across grounds show under the equilibrium fish density assumption that effort will be distributed as a ratio of local attraction weights to the sum of these weights over grounds. To simplify the mathematical presentation below, we sum biomass across species within each ground to examine the total available biomass B_j on the ground; it is to be understood that mean price p_j per biomass will vary among grounds due to variation in the species/size composition of B_j.

Assume that ground j has area fished A_{a_j} nmi^2 and that fish on this ground are mixing with fish from a surrounding area A_{u_j} nmi^2. Let $D_j = B_j/A_{a_j}$ be the mean available biomass density on the grounds (summed over species), and let $D_j^* = B_j^*/A_{u_j}$ be the density of fish in unfished areas surrounding the ground. Assume that at any moment the unfished biomass B_j^* is much larger than B_j, so that B_j^* is depleted slowly relative to B_j should effort on ground j be high (this assumption is almost certainly correct for at least the most intensively fished parts of every trawl ground in B.C., probably for all species as well). We can then write a differential equation for short-term (day–month scale, too short for total biomass $B_j^* + B_j$ to change much) dynamics of B_j, including only mixing and harvest processes:

$$\text{(A1)} \quad dB_j/dt = m_j B_j^*/A_{u_j} - m_j' D_j - K_s e_j D_j/A_{a_j}$$

where m_j and m_j' represent mixing rates ($m_j B_j^*$ is biomass movement rate of fish onto the grounds from A_{u_j}; $m_j' D_j$ is movement off the grounds), e_j is effort in trawl hours, and $K_s e_j/A_{a_j}$ is the local instantaneous fishing mortality rate (area swept per time divided by area of the ground). Under this model, B_j will move rapidly to equilibrium with e_j provided the m_j are large (e.g., 10/year or more), and setting $dB_j/dt = 0$ in eq. A1 allows us to solve for a predicted short-term equilibrium relationship between fishable biomass density, unfished biomass, and effort:

$$\text{(A2)} \quad D_j = m_j B_j^*/A_{u_j}/(m_j' + K_s e_j/A_{a_j}).$$

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At this equilibrium, short-term profitability per trawl hour for fishing in area j, P_j, should be proportional to price and D_j:

$$(A3) \quad P_j = p_j K_s D_j = (p_j m_j K_s B_j^*/A_{u_j})/(m_j' + K_s e_j/A_{a_j}).$$

Note that this profitability is predicted to be proportional to dispersal rate of fish onto the ground (m_j) and to biomass density B_j^*/A_{u_j} "surrounding" (off) the ground and to be inversely proportional to effort density e_j.

Next, assume that fishers adjust the e_j so as to make every area equally profitable, i.e., $P_j = P_0$ for every j where P_0 is a ground-independent base profitability at short-term effort equilibrium. Substituting P_0 into the equilibrium relationship (eq. A3), we can then solve eq. A3 for the short-term equilibrium effort density e_j on each ground:

$$(A4) \quad e_j = (A_{a_j}/K_s)[(K_s p_j m_j B_j^*/A_{u_j})/P_0 - m_j'].$$

This relationship makes intuitive sense, asserting that more effort should be attracted to larger grounds (bigger A_{a_j}), grounds with higher "fish-shed" biomasses B_j^*, and grounds with lower emigration rates m_j'. Note that a hidden assumption in this relationship is that e_j is not large enough to cause substantial changes in mean prices p_j due to short-term changes in the species composition of D_j (e.g., depletion of species i in D_j having low component immigration rates m_{ij}. There is no evidence that such changes in p_j should be a matter of serious concern; FISHMAP plots of seasonal changes in local species CPUE in relation to seasonal effort changes do not show any species being differentially depressed during periods of high effort.

Suppose now that we sum the predicted equilibrium efforts e_j from eq. A4 over grounds and require that these total to a known overall effort $E = \Sigma_j e_j$. Substituting the eq. A4 predictions of e_j into this E constraint results in a relationship that we can solve for P_0:

$$(A5) \quad P_0 = [\Sigma_j w_j B_j^*]/(E + \Sigma_j g_j)$$

where the local parameters w_j and g_j are defined by

$$(A6) \quad w_j = A_{a_j} p_j m_m / A_{u_j}$$

$$(A7) \quad g_j = A_{a_j} m_j' / K_s.$$

Substituting the eq. A5 expression for P_0 into the local effort prediction eq. A4 for each area and using the eqs. A6 and A7 definitions for w and g, we conclude finally that local effort should vary as

$$(A8) \quad e_j = \frac{w_j B_j^*}{\sum_j w_j B_j^*}[E + \sum_j g_j] - g_j.$$

Notice that this equation is the same as the effort model eq. 3 except that each local effort e_j is modified by the ground size-dispersal effects g through the difference

$$(A9) \quad \frac{w_j B_j^*}{\sum_j w_j B_j^*} \sum_j g_j - g_j.$$

The effect of such differences is to cause larger differences in effort between areas than would be predicted from the gravity model component of eq. A8, i.e., the gravity model spreads effort over grounds more evenly than eq. A8 predicts. Thus, in using eq. 3, we assume that this difference can be neglected. We could include the eq. A9 effect in the simulations by making arbitrary but reasonable assessments of m_j' (the A_{a_j} and K_s are "known"), but spreadsheet tests suggest that we need not bother to do so provided local F's ($K_s e_j/A_{a_j}$) are relatively high (as indicated in the FISHMAP analysis). Further, spreadsheet tests indicate that if necessary for future analyses, we can model effort concentration effects caused by eq. A9 terms without having to estimate the g_j by replacing the wB weights in eq. A8 with powers >1.0 of these weights (e.g., make attractiveness of ground j be $(w_j B_j)^3$); using higher powers causes simulated effort to concentrate more violently on attractive grounds.

Appendix 2. Estimation of unfished and current biomass by species and ground using historical catch, qualified CPUE, minimum biomass, and survey data

We assembled catch and qualified CPUE time series for 1954–1996 for each of the grounds in Fig. 4 from logbook records in the Pacific Biological Station trawl database (thanks to Jeff Fargo and Mark Saunders, Pacific Biological Station, Nanaimo, B.C., for help with this). For most years, data were available only at the minor statistical area and locality scale; in the relatively few cases for which a minor–locality area cuts across more than one of the Fig. 4 grounds, we apportioned catch from such minor–locality areas to our grounds in proportion to relative area of each of our grounds included in the statistical area.

We then used an observation error, Bayesian estimation procedure recommended in Walters and Ludwig (1994) for each of the stock/ground combinations analyzed with FISHMAP. The only process errors included in the analysis are the recruitment anomalies estimated for a few species from age-structured analyses. For a range of $B_{ij,0}$ values, we simulated the delay-difference model from 1954 to 1996, subtracting "observed" catch from the simulated population each year. For each $B_{ij,0}$, this results in a calculated biomass time series, $B_{ij,t}$. We then assigned a Bayes posterior probability to each $B_{ij,0}$, assuming equal prior probability for every $B_{ij,0}$, so that the posterior probability was proportional to the product of three likelihood terms:

$$(A10) \quad P(B_{ij,0}|Y) = L^{(\text{CPUE})} L^{(\text{survey})} L^{(\text{FISHMAP biomass})}$$

where Y represents the data set for which likelihoods are calculated and each of the L likelihood terms represents a marginal likelihood for one data type integrated over nuisance parameters of an observation model for that data type. For stocks lacking survey data (at present, all stocks except POP in Goose Island Gully), we set the survey likelihood component $L^{(\text{survey})} = 1.0$. The following paragraphs describe how the likelihood terms are calculated.

The likelihood for qualified CPUE $L^{(\text{CPUE})}$ is calculated by assuming (perhaps unwisely) that qualified CPUE $y_{ij,t}$ for t = 1980–1995 has been proportional to a power β of biomass, i.e., $y_{ij,t} = q_{ij} B_{ij,t}^{\beta} \exp(v_{ij,t})$ with observation errors $v_{ij,t}$ normally distributed. $\beta < 1$ represents admitting possible "hyper-

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stability" in CPUE due to nonrandom search or inappropriate qualification procedures. We assume a uniform prior probability for β between 0.0 (no information about biomass in CPUE) and 1.0 (CPUE proportional to biomass), a uniform prior for $\ln(q)$, and a Jeffreys prior ($1/\sigma$) for the observation variance. We calculate the marginal likelihood "kernel" integrated over β, q_{ij}, and the CPUE observation variance, given the CPUE data, in two steps. We first use the Walters and Ludwig (1994) result for integration over q and σ to obtain an analytical integral over these parameters for fixed β, $SS^{-(17-1)/2}$, where SS is given by

$$\text{(A11)}\quad SS = \sum_{t=1980}^{t=1996} (Q_{ij,t} - \overline{Q}_{ij})^2$$

$$Q_{ij,t} = \ln(y_{ij,t}) - \beta \ln(B_{ij,t})$$

$$\overline{Q}_{ij} = \text{mean of } Q_{ij,t} \text{ over t}$$

where $\overline{Q}_{ij}$ is the maximum likelihood estimate of $\ln(q_{ij})$ conditional on $B_{ij,0}$ (for details on the derivation of eq. A10, see Walters and Ludwig 1994). We then calculate $SS^{-(17-1)/2}$ for a grid of β values (0.0, 0.1,..., 1.0), and $L^{(CPUE)}$ is taken to be simply the sum of these $SS^{-(17-1)/2}$ terms. Note that this simple numerical integration procedure for the nuisance parameters involves dropping all prior probability and likelihood equation terms that do not vary with $B_{ij,0}$ (and hence do not affect comparisons of $P(B_{ij,0}|Y)$ over alternative $B_{ij,0}$ values).

The likelihood component for survey data $L^{(survey)}$ is calculated using the same observation model structure as for CPUE, except we assumed that surveys have been designed so that β = 1.0. Equation A11, with survey estimates as $y_{ij,t}$ instead of CPUE, is used to provide an integrated likelihood over survey catchability and variance parameters. This method of using the survey data makes no prior assumption about limits on the survey q, i.e., about the proportion of the stock seen in survey trawls and the surveyed area.

The likelihood component for minimum 1996 biomass estimates from FISHMAP spatial analysis, $L^{(FISHMAP\ biomass)}$, is calculated by assuming that expanded FISHMAP estimates $k_{ij,1996}B^*_{ij,1996}$ are actual biomass $B_{ij,1996}$ times a lognormally distributed measurement error $\exp(v_{ij,1996})$, i.e., $k_{ij,1996}B^*_{ij,1996} = B_{ij,1996}\exp(V_{ij,1996})$. We assume equal prior probabilities for all $k_{ij,1996}$ values between 1 and 10, i.e., for FISHMAP estimates to average anywhere between 10 and 100% of actual total biomass or for actual biomass to be anywhere from one to 10 times the FISHMAP estimate. From analysis of variation among 1994–1996 FISHMAP biomass estimates for stocks that did not likely change much over the 1994–1996 period, we estimate the standard deviation of $v_{ij,1996}$ to be on order $\sigma_v = 1.3$ (sample sizes for FISHMAP assessment are too small to provide reliable estimates of σ by local stock). Under these assumptions, the marginal likelihood for $B^*_{ij,1996}$ integrated over $k_{ij,1996}$ is proportional to the difference between two cumulative normal probabilities, so that

$$\text{(A12)}\quad L^{(FISHMAP\ biomass)} = N[\ln(1.0\,B^*_{ij,1996}/B_{ij,1996})/\sigma_v] - N[\ln(1.0B^*_{ij,1996}/B_{ij,1996})/\sigma_v]$$

where $N[x]$ is the normal distribution function evaluated at standard deviate x (e.g., $N[-1.96] = 0.025$, $N[1.96] = 0.975$, etc.). Note that this method only assigns low marginal likelihoods to $B_{ij,0}$ values for which $B_{ij,1996}$ is calculated to be very high (>>10 times) or low (much less than one time) compared with the FISHMAP biomass estimates, so that the FISHMAP estimates are really only used to help limit the range of probable $B_{ij,0}$ values. We could in principle have included all the FISHMAP biomass estimates for 1994–1996 in an SS likelihood function as for CPUE and survey data; however, we know that the 1994–1995 logbook data may not be comparable with the 1996 data, and in any case the 1994–1995 data have already been "included" in the $L^{(CPUE)}$ part of the assessment.

The "best" point estimate of $B_{ij,0}$ is taken to be the one that maximizes P in eq. A10. By summing the P values over $B_{ij,0}$ grid points, we can also easily find the "risk averse" estimate $B_{(0.2)ij,0}$ for which the cumulative posterior probability of $B_{ij,0}$ is 0.2 (80% chance that the data came from a $B_{ij,0}$ larger than $B_{(0.2)ij,0}$, assuming that the observation model for $y_{ij,t}$ is structurally correct about q_{ij} being constant).

The catchability estimate $\exp(\overline{Q}_{ij})$ cannot be used to predict catches from biomass and total effort on ground j, since it is inflated through the use of qualified effort in the assessment of qualified CPUE. We estimate the fishery catchability coefficient for total effort E_{jt} conditional on any calculated biomass time series as

$$\text{(A13)}\quad q_{ij} = \Sigma_t C_{ij,t}/\Sigma_t B_{ij,t}E_{jt}$$

where the t sums are over 1980–1996, $C_{ij,t}$ is measured catch of species i on ground j in year t, E_{jt} is measured total effort on the ground, and $B_{ij,t}$ is the calculated biomass time series given $B_{ij,0}$ and observed catches (this estimator is the conditional maximum likelihood estimate assuming additive normal errors in the prediction relationship $C_{ij,t} = q_{ij}B_{ij,t}E_{jt}$).

Note that this assessment method uses only the trends in qualified CPUE and surveys to compare alternative estimates of $B_{ij,0}$. For every possible $B_{ij,0}$, the mean $\overline{Q}_{ij}$ "removes" scale differences between Y and B from the SS, so higher SS values (poorer fit to data) can occur only for $B_{ij,0}$ values that produce a $B_{ij,t}$ trend pattern different from the $y_{ij,t}$ trend pattern. For cases where the $y_{ij,t}$ lack any trend (a common pattern), the method indicates that $B_{ij,0}$ must have been so large that the historical catches did not reduce $B_{ij,t}$ (P is maximized at highest $B_{ij,0}$ grid point). It is obviously risky to use the method for such cases, except to provide a minimum estimate of $B_{ij,0}$ large enough to have at least produced the observed catches without $B_{ij,t}$ being driven to zero. The method can also result in overestimates of $B_{ij,0}$ for stocks that have had high recruitment variation in conjunction with high exploitation rates, like Pacific cod; in such cases, deterministic (observation error) simulations of $B_{ij,t}$ are driven to zero when high observed catches (that were actually due to unusually high recruitments) are subtracted from the simulated biomass.

Note further that the main information about $B_{ij,0}$ in more complex age-structured assessment procedures also comes from survey or CPUE SS terms like the one in eq. A11. Age composition data mainly provide information about recruitment variation and age selectivity. Even total mortality rate Z is poorly determined in most age composition data due to confounding of age selectivity and mortality effects, and

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even when Z is well determined the F and M components of it rarely are. We are in effect using the age composition data wherever possible by including recruitment anomaly estimates in the delay-difference simulations, but we avoid the very dangerous assumption that F (and hence stock size) can be measured through apparent changes in Z.

Appendix reference

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Modeling environmentally driven uncertainties in Baltic cod (*Gadus morhua*) management by Bayesian influence diagrams

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Abstract: The large variability in Baltic cod (*Gadus morhua*) recruitment has been attributed both to environmental factors dependent on the inflow of saline water (oxygen and salinity in spawning deeps) and to the size of the spawning stock. Due to the complex interactions between hydrographic and biological processes, future recruitment levels of cod will remain highly uncertain and increase uncertainties in stock predictions and management advice. We assessed the effects of the exploitation level and mesh size used by a trawl fishery on some variables of management interest under different environmental conditions. The modeling consisted of three separate steps: (*i*) modeling of selectivity, (*ii*) estimation of uncertainties by Monte Carlo simulations, and (*iii*) decision analysis by Bayesian influence diagrams, focusing on the structural uncertainties and model selection. Realistic assumptions of environmental conditions and present fishing mortality rates suggest that the current Baltic cod fishery is unsustainable. We use our approach to identify robust management measures that reduce the risk of overfishing and the sensitivity to management information. The value of information analysis demonstrates the advantages of a larger mesh size as a management measure.

Résumé : La grande variabilité dans le recrutement de la morue franche (*Gadus morhua*) de la Baltique a été attribuée à des facteurs environnementaux qui dépendent de l'apport d'eau salée (oxygène et salinité dans les profondeurs où s'effectue la fraye) et à la taille du stock de géniteurs. En raison des interactions complexes entre les processus hydrographiques et biologiques, les niveaux futurs de recrutement chez la morue resteront très incertains, ce qui accroîtra les incertitudes dans les prévisions des stocks et les recommandations en matière de gestion. Nous avons évalué les effets du niveau d'exploitation et du maillage utilisé par les chalutiers sur certaines variables prises en compte dans la gestion des stocks dans différentes conditions environnementales. La modélisation a été effectuée en trois étapes distinctes : (*i*) modélisation de la sélectivité, (*ii*) estimation des incertitudes par des simulations de Monte Carlo et (*iii*) analyse de décision au moyen de diagrammes d'influence Bayésiens, qui se concentrait sur les incertitudes structurales et le choix du modèle. Selon des hypothèses réalistes sur les conditions environnementales et les taux présents de mortalité par pêche, la pêche actuelle de la morue de la Baltique n'est pas viable. Nous utilisons notre approche pour concevoir des mesures de gestion énergiques qui réduisent le risque de surpêche et la sensibilité à l'information de gestion. L'analyse fondée sur la valeur de l'information montre que l'agrandissement du maillage est une mesure de gestion bénéfique.

[Traduit par la Rédaction]

Introduction

Uncertainty has become an important feature of fisheries assessment and management (Pearse and Walters 1992; Ludwig et al. 1993; Hildén 1997*a*). The aim of decision analysis in resource management is to provide an overview of the relevant uncertainties and their possible impact on management decisions. In the face of uncertain management problems, scientists frequently stress the importance of research, which easily leads to data gathering in cases where action is needed. The key task in fisheries management is to choose the correct action, not to try to predict uncertain quantities like catch or biomass.

Uncertainty is reflected in the development of precautionary approaches to fisheries management (FAO 1995) and in the general interest in risk assessment (Smith et al. 1993). At

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the methodological level, we need to develop methods and approaches that allow for the systematic treatment of uncertain information in the system to be managed. For example, the inclusion of a stock-recruitment (S/R) relationship that can be based on several types of models is a demanding task, as is the inclusion of environmentally driven variations in recruitment.

The recognition of uncertain information might substantially change our perception of the present state of resources and their exploitation compared with modeling by deterministic point estimate models. Ludwig (1996*a* and 1996*b*) concludes that, maximum likelihood methodology, being based on point estimate parameters, grossly underestimates the risk of stock collapse. Moreover, Cook et al. (1997) have shown for North Sea cod (*Gadus morhua*) that, due to estimations errors, even regimes close to maximum sustainable yield can be risky.

From the decision-making point of view, it is essential to analyze the sensitivity of managerial decisions to uncertainty. Some management strategies may be more information robust than others and some may be able to diminish future uncertainties more effectively than others. The findings of MacLennan et al. (1992) and MacLennan (1995), for example, suggest that managers should pay more attention to exploitation level and selectivity pattern in variable fisheries than they would in stable fisheries with low recruitment uncertainty. Moreover, Myers and Mertz (1998) underlined the importance of control of selectivity in a precautionary fishery and recommended a spawn-at-least-once policy, whereby fish would become vulnerable to commercial gear only after they have spawned once.

Here, we analyze the effects of uncertainty on the management of the Baltic Sea cod fishery. We examine how environmentally driven uncertainties in recruitment and growth may affect cod management. Our approach uses Bayesian influence diagrams as metamodels to combine different sources of uncertain information, including three different recruitment models.

Influence diagrams are used to describe uncertain decision problems (Schachter 1986; Oliver and Smith 1990). They are decision-oriented Bayesian belief nets (Jensen 1996) that include at least one decision variable (a decision variable means that the value of the variable can be chosen by the decision-maker and implemented by some action) and an objective function, which is either minimized or maximized by the decision variables. The dependence of variables on each other is described by conditional probabilities. Influence diagrams are closely related to decision trees, but the graphical construction of the model allows the use of expert knowledge in planning the model structure in a more effective way.

The advantage of analyses with decision trees (McAllister and Peterman 1991) or influence diagrams is that they focus on the relationship between action and knowledge, and so encourage us to examine the options for actively managing an uncertain system and to conduct systematic studies on how information can support management. Clemen (1991) gave general examples of the use of influence diagrams in decision analysis. Pradhan et al. (1996) have shown that belief networks are not sensitive to the imprecision in the input probabilities and can be classified as "robust tools".

Bayesian decision analysis by metamodels (models including the information content of several models) is still a relatively new area in fisheries management. Bayesian analysis tends to focus on parameter uncertainties (see Punt and Hilborn 1997 and references therein), although structural uncertainty is usually considered more crucial (Francis and Shotton 1997; Punt and Hilborn 1997; Charles 1998). There are some applications for Bayesian belief networks and influence diagrams in fisheries and environmental problems (Varis et al. 1990; Hildén 1997*b*; Varis and Kuikka 1997; Heikinheimo and Raitaniemi 1998). A practical advantage of belief network models is that they can be used interactively in discussions between stakeholders in fisheries negotiations. They can also be used to demonstrate graphically the effects of various assumptions on the probability distributions of variables of interest.

The shapes of the probability distributions convey the quality of information in Bayesian decision analysis (e.g., Clemen 1991) and allow us to assess the importance of the uncertainties. Moreover, the actors involved in fisheries management may have different risk attitudes, and consequently, a scientific analysis should support discussions of acceptable risk levels on the basis of probability distributions. Such discussions could possibly lead to management systems that are more information robust (Charles 1998) and thus less sensitive to yearly managerial decisions and monitoring uncertainties than are systems based solely on total allowable catches (TAC).

Baltic cod fishery as a management problem

An uncertainty analysis of the Baltic cod fishery is of general interest, as the Baltic Sea offers good conditions for analyzing fisheries management and environmental interactions. The Baltic Sea ecosystem is a simple one with a limited number of species (Elmgren 1984). Cod is the dominant piscivore and a wealth of data are available on both the Baltic environment and its dominant fisheries. Since 1974, all major fisheries have been regulated by an international convention of the permanent International Baltic Sea Fishery Commission in Warsaw.

The yearly average catch of the Baltic cod fishery has been around 200 000 t (Anonymous 1997). Recruitment to the fishery was, due to favorable environmental conditions and reasonable spawning biomass, exceptionally good in 1977–1982. As a result, landings in 1980–1985 were above 300 000 t. Both gill nets and trawls are used, but fishery statistics do not give exact data on the distribution between these gears. The information available indicates that in recent years the gillnet catch has accounted for around 40% of the total catch in weight (E. Aro, Finnish Game and Fisheries Research Institute, P.O. Box 6, FIN-00721 Helsinki, Finland, personal communication).

The Baltic Sea cod population is unique among cod populations in its ability to reproduce at a minimum salinity of only 11‰ (Westin and Nissling 1991; Nissling et al. 1994). In the Baltic Sea, water of this or a higher salinity occurs only in some deep areas, where the oxygen content is often too low for the successful development of eggs. This prob-

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Table 1. Estimated fishing mortalities (1/year) at age for the two growth rates considered.

Age (years)	Slow growth	Fast growth
1	0.0095	0.0095
2	0.092	0.13
3	0.55	0.45
4	0.65	0.69
5	0.73	0.66
6	0.68	0.58
7	0.60	0.54
8	0.55	0.52
9	0.52	0.51
10	0.51	0.50
11	0.50	0.50

Note: In these examples the fishing effort is assumed to be at the estimated present level. A 120-mm cod end is assumed in the trawl fishery and 105-mm mesh size in the gillnet fishery.

lem has been aggravated by anthropogenic eutrophication (Hansson and Rudstam 1990).

Due to a combination of an intensive fishery (Sparholt 1996) and highly variable hydrographic conditions affecting the volume of water suitable for successful spawning and egg development (spawning volume (SPVOL), Pliksh et al. 1993), the Baltic cod stock biomass has changed substantially over the past two decades. Current data on SPVOL show remarkable yearly variations. These are caused partly by the unstable oxygen demand arising from the complicated eutrophication process and partly by the unpredictable inflow of saline water (Matthäues 1993). Therefore, future uncertainties are bound to be considerable.

Despite the simplicity of the ecological system of the Baltic Sea, management of the Baltic cod fishery is complicated by the network of environmental and human interactions involved, as indeed are fisheries in general. We lack exact knowledge of causalities, state variables, and parameters (such as fishing mortality, exact stock dynamics, stock size, and the future quality of the water). Management uncertainties arise in a variety of ways, for example, in misreporting of catches, which is probably significant for Baltic cod (Anonymous 1996). Misreporting affects the quality of the assessments and also the implementation efficiency of management measures based on TAC's. As Rosenberg and Brault (1993) pointed out, such a dependency between implementation uncertainty and assessment uncertainty is dangerous.

Materials and methods

Modeling approach

With Baltic cod, the decision problem in our analysis is whether or not a change in mesh size would benefit the fishery. Moreover, fishing mortality can be controlled by the TAC system. Fisheries managers are assumed to be interested in future catches and recruitment risks or, alternatively, in the possible need to close the fishery when the spawning biomass is too low. From the modeling point of view, the task is to model the effects of the two decision variables (mesh size and fishing mortality) on the interest variables and to demonstrate how sensitive the advised actions are to the relevant scientific uncertainties.

The analysis consisted of three main steps. First, we calculated deterministically the selection process of the two types of selective gear (trawl and gill net) using a model based on length distributions. Second, we estimated the effects of alternative hypotheses about the recruitment process on the variables that managers tend to focus on (catch, biomass, etc.) using an age-structured model and Monte Carlo simulations. This step produced probability distributions of the interest variables (e.g., catch and biomass) that are conditional on the recruitment hypotheses. Third, we used these conditional probability estimates in a Bayesian influence diagram model to combine the uncertainty estimates of the different models. This step leads to an analysis of the role of different information sources and hypotheses from the point of view of decision-making. The focus of the whole analysis is on structural uncertainties, not on the estimation of parameter uncertainty.

Basic population parameters and the selection process

We assumed that the age-specific fishing mortality rates depend on fishing effort, gear selectivity properties, and age-specific length distribution. In the Baltic, cod is mainly caught with trawls and gill nets. We modeled the effects of different combinations of these gear types on the size distributions of the cod population by combining the length-specific retention rates of the two gear types with the length distributions at age. This procedure gave gear- and age-specific mean weights for different fishing mortality rates and spawning biomass at age. We used these values as input values in the Monte Carlo simulations (see below).

The selection model uses discrete age-classes, and growth takes place in one step at the beginning of the year. We assumed that all surviving fish in an age- and length-class grow at a constant rate. Thus the standard deviation in length at age is constant and independent of age. The coefficient of variation (CV) of the length distribution of age group 1 was set to 35%, which leads to CV values comparable with those reported for older age-classes by Sparholt (1993).

We calculated the fishing mortality rate at a certain length-class by multiplying the fishing mortality of the fully recruited length-class by the length-specific retention rate (Pikitch 1987):

$$(1) \qquad F(l,g) = F(g)\cdot r(l,g)$$

where $F(l,g)$ is fishing mortality rate of length-class l in gear g, $F(g)$ is fishing mortality of the fully recruited length group in gear g, and $r(l,g)$ is retention rate of length-class l in gear g ($r(l,g) \leq 1$). We used the retention rate data of Tschernij et al. (1996) for 120- and 140-mm diamond mesh sizes in trawls. For the gillnet fishery, we used a stretched mesh size of 105 mm, which is the smallest permitted by Baltic Sea fishing rules. Selectivity data for the gillnet fishery have been produced by the Danish Institute for Fishery Technology and Aquaculture (unpublished).

The F values of gillnet and trawl fishing were calculated using the proportion of 40% gillnet catch as a fixed constant. Gear- and age-specific F values were calculated using the length distribution model and the retention data. The mean growth rate, mean recruitment, and mean yield reported in Anonymous (1996) for 1976–1995 were used as input data in this estimation procedure. The sum of squares of the difference between the calculated F values and the values reported in Anonymous (1996) for age-classes 3–7 was minimized. This procedure gave age-specific F values in reasonable agreement with the information available on mortality, yield, growth, and selectivity (Table 1). Thus, the above estimation approach is heavily based on the information obtained from selectivity data but also includes information from virtual population analysis. We used these F values to represent the present situation.

The total instantaneous mortality of length-class l in age-class a was

$$(2) \qquad Z(a,l) = F(l,\text{gillnet}) + F(l,\text{trawl}) + M(a)$$

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Table 2. Calculated weight at age in the population without fishing and weight at age in the catches and in the population at present fishing pressure at the two growth rates considered.

			Weight at age: present fishing					
	Weight at age without fishing		Slow growth			Fast growth		
Age (years)	Slow growth	Fast growth	Gillnet	Trawl	Population	Gillnet	Trawl	Population
1	0.062	0.062	0.17	0.16	0.06	0.17	0.16	0.06
2	0.24	0.29	0.46	0.37	0.24	0.55	0.42	0.29
3	0.77	0.67	0.88	0.78	0.73	0.83	0.69	0.63
4	1.0	1.6	0.93	0.93	0.88	1.2	1.5	1.4
5	1.4	1.7	1.0	1.2	1.2	1.3	1.6	1.5
6	1.9	2.5	1.3	1.7	1.7	2.2	2.4	2.4
7	2.4	3.6	1.9	2.2	2.2	3.0	3.5	3.5
8	3.3	4.3	2.6	3.1	3.1	3.5	4.1	4.1
9	4.6	5.2	3.5	4.4	4.4	4.2	5.0	5.0
10	5.2	7.6	3.9	5.0	5.0	5.8	7.4	7.4
11	5.8	9.8	4.3	5.6	5.6	7.3	9.6	9.6

Note: A 120-mm cod end is assumed in the trawl fishery and 105-mm mesh size in the gillnet fishery.

Table 3. Crucial input values of simulations.

Natural mortality (M) (1/year)	0.2
Fishing mortality of trawl fishery for totally recruited length-class (1/year)	0.50
Fishing mortality of gillnet fishery for maximally recruited length-class (1/year)	0.65
Length of fish at beginning of maturation year (cm)	40
Length–weight relationship $W = aL^b$	
a	0.0102
b	3.00
Survival of trawl escapees (%)	100
Mean length of 1-year-old fish (cm)	16.4
CV of length of 1-year-old fish	0.35
Gillnet catch as proportion of total catch (%)	40

Note: Fishing mortalities refer to the length-class with the highest retention rate.

where $M(a)$ is natural mortality rate at age a. We assumed that the natural mortality rate was 0.2·year^{-1} for fish of age 3 years and older (Anonymous 1996). Recruitment was modeled by S/R models for 1-year-old fish, and we took the cannibalism in age-classes 1 and 2 into account by using the equations obtained from a multispecies virtual population analysis of Baltic cod (Sparholt 1995) for age-classes 1 and 2:

$$(3) \quad M(1) = 6.76 \times 10^{-7} \times \mathrm{SSB3} + 0.2$$

$$(4) \quad M(2) = 1.502 \times 10^{-7} \times \mathrm{SSB3} + 0.2$$

where SSB3 is spawning biomass (thousands of metric tons) of fish 3 years and older.

The number of fish in length-class l in age group a was calculated by

$$(5) \quad N(a,l) = N(a-1,l-\mathrm{inc}(a))\cdot\exp(-Z(a-1,l-\mathrm{inc}(a)))$$

where inc(a) is the increment of length in 1 year in age group a.

The catch in gear g was calculated according to the following equation:

$$(6) \quad C(a,l,g) = F(l,g)\cdot N(a,l)\cdot(1-\exp(-Z(a,l)))/Z(a,l).$$

We used a mean value from Bagge and Steffensen (1991) to convert fish length (centimetres) to weight (grams):

$$(7) \quad W = 0.010197\cdot L^3.$$

We used two different growth rates in the analysis. It is impossible to say with confidence what the future rate will be, but it is still of interest to establish whether or not the uncertainty about growth would lead to different management decisions. We therefore applied two growth scenarios, one for "slow growth" and one for "fast growth". Our source of information was the mean weight at age in Anonymous (1996, table 3.7). The data given there reflect past selectivity and fishing mortality rates. We corrected them to correspond to the size distributions in unfished populations to obtain a starting point for simulations of different fishing alternatives (Table 2). We did this by finding increments in growth of length that gave the observed mean weight at age with the present fishing mortality. Removing the effects of selective fishing from the model described above gave the weights at age in Table 2. Thus, these weight at age numbers are based on eq. 7. The correction did not take into account any additional density-dependent effect on the growth rates. The present growth rate (in 1997) is close to the fast growth scenario. The most important input values are given in Table 3.

We used the above equations (without cannibalism) to calculate the yield per recruit (Y/R) results to demonstrate the dependence of the results on growth, selection, and natural mortality. We further used the S/R and cannibalism information in Monte Carlo simulations to estimate the management uncertainties caused by an uncertain S/R relationship.

Recruitment models

We modeled recruitment in three different ways, referred to here as the random model, the Ricker model, and the environmental Ricker model.

Random model

This model samples recruitment of 1-year-old cod randomly from the historical recruitment values given in Sparholt (1996). There is no positive effect of the spawning stock biomass on the recruitment, but cannibalism (eqs. 3 and 4) caused some autocorrelation behavior in the biomass of the stock.

Ricker model

We used the model parameters estimated by Sparholt (1995) for the relationship between the spawning stock biomass and 1-year-old cod. The Ricker model is

$$(8) \quad R = A\cdot\mathrm{SSB}\cdot\exp(-B\cdot\mathrm{SSB})$$

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Fig. 1. Example of the sampled recruitment values of 1- and 3-year-old fish of the same year-class using the environmental Ricker model. The values were calculated with the present fishing mortalities.

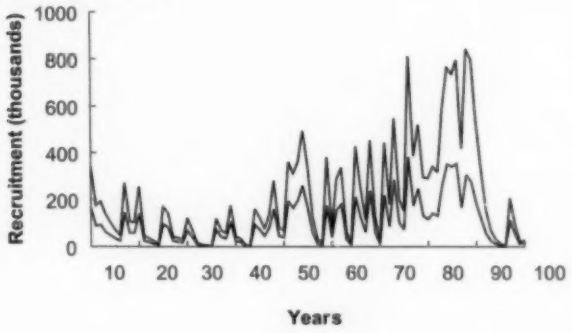
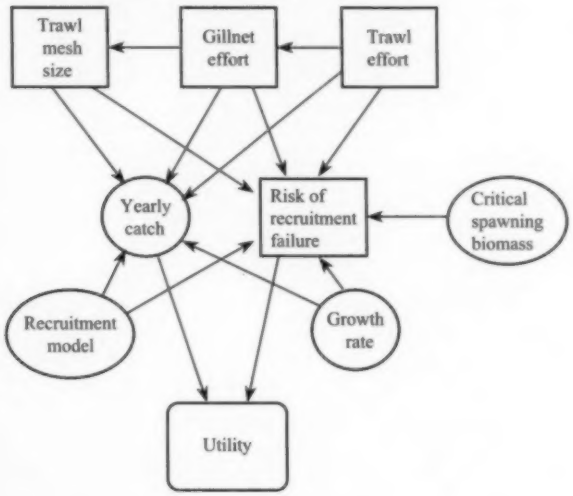


Fig. 2. Influence diagram model used in the analysis. It contains only the most important input and output parameters of Monte Carlo simulations. An arrow from one decision to another implies the order of the decisions.



where A and B are parameters from Sparholt (1995) and SSB is spawning biomass. Cannibalism was taken into account as described above by eqs. 3 and 4. To simulate the variation in recruitment, we assumed a CV of 30% for both parameters in the Ricker function. Yearly values were sampled separately from the distributions without autocorrelation. An implicit assumption is that the water quality in the Baltic will remain at least as good as it has been historically.

Environmental Ricker model

This model mimics the fluctuations caused by influxes of high-salinity water and the decrease in SPVOL (Pliksh et al. 1993) after a pulse. SPVOL is a measure of the amount of water in which spawning can succeed, taking into account the salinity and oxygen requirements of cod. The occasional pulses of oxygenated saline water into the Baltic are important for large-scale improvements of oxygen conditions in the deeps and have a direct influence on SPVOL. Both the frequency and magnitude of the pulses are important. Current environmental knowledge suggests that eutrophication of the Baltic Sea increases oxygen consumption in the deeps (Möller and Hansen 1994; Matthäues and Lass 1995). Our model assumed that the frequency and magnitude of the saline pulses will remain at present levels, but that they will not improve the spawning conditions of cod as before, owing to increased eutrophication. We assumed that, in terms of cod recruitment, the mean water quality in future will be 30% lower than it has been historically. However, this mean level was assumed to be the same over the whole simulated time horizon, without further deterioration.

Technically, we modified parameter A of the Ricker model to reflect the trends and variability observed historically in water quality. The distribution of the parameter was set to describe changes in the historical data on SPVOL (data given in Sparholt 1996). The yearly values of A were determined with the aid of a dummy variable having the values "saline pulse" or "no pulse" with respective probabilities 0.4 and 0.6. When the value "saline pulse" was obtained, we took the value of parameter A from a lognormal distribution where the expected values of parameters were from Sparholt (1996) and CV was assumed to be 0.3 (same as the Ricker model above). When the value of the dummy variable was "no pulse", we determined the value of SPVOL from the previous year's value, following the rate of decline observed in SPVOL in the absence of saline pulses. The average rate of decline was 42%·year^{-1}, but using the histogram function of @Risk software (an add-in program for Monte Carlo simulations (http://www.palisade.com/index.html)), we created probability distributions for the decline that were the same as those observed in the data. Parameter B had a CV of 30%, which is the same as in the Ricker model above. Figure 1 gives an example of one set of recruitment values and demonstrates the effects of cannibalism on the year-class dynamics of 3-year-old cod.

Table 4. Probabilities of prior variables in the influence diagram model.

Prior variable	Alternatives	Probability
Recuitment model	Random	0.1
	Ricker	0.3
	Environmental Ricker	0.6
Growth rate	Fast	0.7
	Slow	0.3
Critical spawning biomass (t)	240 000	0.7
	480 000	0.3

Monte Carlo simulations

The aim of the Monte Carlo simulations was to produce the conditional probability distributions of interest variables (yield, probability of biomass being below a certain threshold). The conditioning variables used as uncertain prior variables in the influence diagram model were growth rate, recruitment model, and critical spawning biomass. Simulations were made separately for all combinations of the discrete prior and decision variables of the influence diagram model (Fig. 2; Table 4). There were a total of 300 separate simulations (2 growth rates × 3 recruitment models × 2 mesh sizes × 5 gillnet F values × 5 trawl F values). In each simulation, we made 400 iterations over 110 years to estimate the probability distributions of catch, biomass, and the probability of biomass being under the levels assumed to be critical. For the environmental Ricker model, we ran 600 iterations owing to the more unstable behavior of the model. This number of iterations gave quite stable expected values and variances; additional iterations did not improve the estimates substantially. When estimating the distributions of the interest variables (catch, biomass), we discarded the first 10 years to avoid the effects of the initial values. The follow-

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Table 5. Utility function used in the basic influence diagram.

	Risk level				
Yield (kt)	0.0–0.2	0.2–0.4	0.4–0.6	0.6–0.8	0.8–1.0
<50	25	23	21	19	17
50–100	75	68	62	56	51
100–150	125	114	103	94	85
150–200	175	159	145	131	120
200–250	225	205	186	169	154
250–300	275	250	227	207	188
300–350	325	295	269	244	222
350–400	375	341	310	282	256
400–450	425	386	351	319	290
450–500	475	432	393	357	324
500–550	525	477	434	394	359
>550	575	523	475	432	393

Note: Risk level is the proportion of years when the spawning biomass falls below the critical spawning biomass. Another influence diagram using only catch as the objective was also evaluated.

ing 100 years were then used to obtain probability distribution estimates for the frequency of low spawning biomass. Long simulations are needed due to the autocorrelation effects.

For the catch, we used the probability distribution of a single year (the 90th year in the simulation model) to describe the long-term interest of managers and fishers. This is the node "early catch" in the influence diagram model. Note that the number of years in the model has an effect on the catch probability estimates (long simulation = more time for stock collapse).

The node "critical spawning biomass" has two values, 240 000 and 480 000 t, for critical biomass (Table 4). These figures were put forward as alternatives for a critical spawning biomass in Anonymous 1996 (section 3.11). It was suggested that the risk for recruitment overfishing would increase markedly were spawning biomass to go under these values. The number of times the spawning biomass fell below the critical level over the 100 years of simulation was used as an index describing the recruitment risk, which is included in the node "risk for recruitment failure" in the influence diagram model.

For the catch, we discretized the probability distributions into 10 classes (<50 000 t, 50 000 – 100 000 t, etc.) and the risk variables into five classes (0–20% of the years, 20–40%, etc.).

Bayesian influence diagram modeling

In influence diagram models, both information and management control are described by probability distributions. Narrow distributions indicate high-quality information or good controllability. In our case the discretized probability distributions obtained from the Monte Carlo simulations were used as input data for the influence diagram analysis. We used Hugin software (http://www.hugin.dk/) based on the Lauritzen algorithm (Lauritzen and Spiegelhalter 1988), which is computationally very effective, as it allowed totally interactive use of the model, even though the model included information from 300 separate Monte Carlo simulations.

Our influence diagram model (Fig. 2) is quite simple. It is a metamodel that combines only the input and output values of the Monte Carlo simulations. The growth level, the recruitment process (the three models explained above), and the critical level of spawning biomass are used as prior variables. The discrete values and probabilities of the prior variables are given in Table 4. The historical data cannot be used to judge the prior probabilities of the recruitment models, which give very distinct ways to describe the recruitment process. A common attitude among water quality scientists is that water quality will continue to deteriorate in the future. The environmental Ricker model is therefore the best justified and we decided to assign it the highest prior probability. The subjective prior probabilities used are given in Table 4. However, as these are very subjective assessments, an extensive sensitivity analysis was carried out for them.

The decision variables are the mesh size of the trawl (120 and 140 mm) and the gillnet and trawl fishing mortalities (F factor with values 0.2, 0.5, 0.8, 1, and 1.3). The F factor is the multiplier of the age- and gear-specific fishing mortality rates. The information contents in the nodes "yearly catch" and "risk for recruitment" are conditional probabilities, e.g., if mesh size is 140 mm, the F factor of the trawl fishery is 1.0, the F factor of the gillnet fishery is 0.8, growth is slow, and the recruitment model is random, then the probability of yield being between 100 000 and 150 000 t is 0.3.

We need an objective or utility function to evaluate the expected performance of the management options. As the first objective function, we used a function of the annual catch and the probability that spawning biomass will fall below a critical level. The number of times the spawning biomass actually fell below the critical level is an indicator of biological risk. High biological risk was assumed to impair the utility of a certain catch (Table 5). As an alternative objective, we used catch only to see to what extent recognition of recruitment risk affects the preferred decisions.

The expected value of perfect information describes the maximum additional utility that could be obtained by knowing the exact value of a variable at the time a decision is taken in contrast with having only uncertain prior information about the variable. If you are given information at the time of decision-making and choose a different action with better outcome, the information led to a better result and had some positive value. The expected value of perfect information is simply the expected difference in the expected value of the utility before and after the true value of the quantity becomes known. In the case of influence diagrams, this "becoming known" can be modeled by adding an arrow from a variable of interest to a decision variable. Calculation of the value of information is described in greater detail in Clemen (1991).

Results

Effects per recruit

When yield potential is estimated on a Y/R basis, there is a substantial difference between the fast and slow growth scenarios (Table 6). At slow growth rates, the optimal F factor combination with the 120- and 140-mm trawl mesh sizes would be 80% of the present trawl fishing mortality and 20% of gillnet mortality, which corresponds to the lowest

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Table 6. Yield (kt) produced by a recruitment of 361 million 2-year-old cod (long-term mean recruitment value (Sparholt 1995)) with different efforts (1 = present value, 0.8 = 0.8 × present value, etc.) for the two growth rates considered.

	Gillnet *F* factor				
Trawl *F* factor	1.3	1	0.8	0.5	0.2
Slow growth					
Mesh size: 120 mm					
1.3	203	205	206	209	212
1	209	212	214	217	221
0.8	214	216	218	222	**227**
0.5	218	220	221	223	225
0.2	206	201	197	188	174
Mesh size: 140 mm					
1.3	223	226	229	234	240
1	226	230	233	239	246
0.8	228	232	235	240	**247**
0.5	226	229	230	233	235
0.2	207	202	197	186	171
Fast growth					
Mesh size: 120 mm					
1.3	239	243	246	251	257
1	252	257	261	267	275
0.8	261	267	271	278	286
0.5	269	274	278	284	**291**
0.2	243	240	237	232	224
Mesh size: 140 mm					
1.3	278	284	289	298	308
1	285	293	298	307	318
0.8	289	297	302	312	**323**
0.5	286	292	297	304	313
0.2	246	243	240	234	225

Note: The highest value is in bold. S/R assumptions are not included in these estimates.

gillnet mortality used in the simulations. At fast growth rates, the optimal amount of fishing with the 120-mm mesh size would be 50% of trawl and 20% of gillnet fishing. In the case of fast growth and the 140-mm mesh size, the optimum would be 80% of trawl mortality and 20% of gillnet mortality. Compared with present fishing mortality rates (*F* factor = 1 and mesh size = 120 mm), the average yield could increase from 257 000 to 323 000 t by increasing the mesh size to 140 mm and by decreasing the trawl fishing intensity to 80% and the gillnet mortality to 20% of the present rate. Note that these figures do not include the effects of cannibalism and S/R knowledge, which are, however, taken into account in all other results.

Effects of S/R hypotheses

Examples of the effects of different recruitment hypotheses on the posterior probabilities of the catch are shown in Fig. 3. With the prior probability values used, the random model gives expected values close to those obtained by the Ricker model. Due to the effect of cannibalism, which restricts the growth of the stock biomass, the Ricker model gives, however, a somewhat narrower distribution. The probability of very strong year-classes is higher in the random model.

The catch distribution obtained by the environmental Ricker model is skewed, with a high probability of low yields, owing to the assumed deterioration in environmental conditions, which diminishes the probability of good recruitment. This changes the perception of stock dynamics significantly. The model suggests that at current fishing intensity, there is a high probability for a yield of under 50 000 t, which is very low compared with the yield potential with lower fishing mortalities.

Combining the probability distributions calculated with the influence diagram model gives us an estimate of the structural uncertainty, i.e., the uncertainty reflected in the choice of recruitment model and its prior weighting (Fig. 3, lower panel). The distributions become flatter because some information is lost when the outcomes of the different models are combined. This is mainly due to the environmental Ricker model, which produces a very different catch distribution with a high frequency of poor yields. It represents a realistic modeling of the environmental effects related to pulses of saline water.

Using the prior probabilities of Table 4 and the utility function of Table 5, we can derive expected utilities for different decision combinations (Table 7). Table 8 shows the expected catches for these combinations. With present mesh sizes, utility could be increased by 40%, from 122 to 178 units; in terms of catches, this corresponds to a 30% change. The change in combined risk–catch utility is larger because of the lower risk associated with reduced mortality rates. If only mesh size were changed, utility would increase by 30% and catch by 25%. If both mesh size and fishing mortality rates were optimized, the greatest increase in utility could be over 60% (catch 47%). These estimates indicate that the yearly loss of catch potential owing to overfishing is 66 000 t.

Sensitivity and decision analysis

We tested the sensitivity of the preferred decisions to the prior probabilities for the recruitment models with models combining both risk and catch in the objective function (Table 5) and with models having only catch as the objective function (Figs. 4 and 5). The preferred decisions and expected catches change when the prior probabilities of the recruitment models are changed. The optimal *F* factors for each combination of prior probabilities and the corresponding catches are given in the figures. For example, the highest probability for the random model is shown in the upper left corner. If one is not willing to change the mesh size and has a strong belief in the random model (no positive feedback from high biomass) and a concern for biological risks (upper left corner in Fig. 4), one would seek to reduce both gillnet and trawl fishing mortality rates by using a trawl mesh of 120 mm; with a trawl mesh size of 140 mm, gillnet mortality rates would be reduced but trawl mortality rates increased by 30%. With catch as the only objective (Fig. 5) the advice for the 120-mm mesh would be to aim for an increase in trawl fishing effort and to reduce gillnet effort, but for the 140-mm mesh the advice would be the same both with and without the risk indicator in the objective function. In the random model (no S/R relationship) the separate risk indicator offers some additional information, compared with

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Fig. 3. Examples of the effects of recruitment models and their probabilities on the posterior distributions of yield. The upper panel gives the yield distributions, assuming that the correct recruitment model is known (probability of model = 1). The lower panel shows distributions that arise when recruitment is due to probability combinations of different models. The combinations are given in the figures. Present fishing effort and present mesh sizes are assumed. Other prior probabilities are as in Table 4.

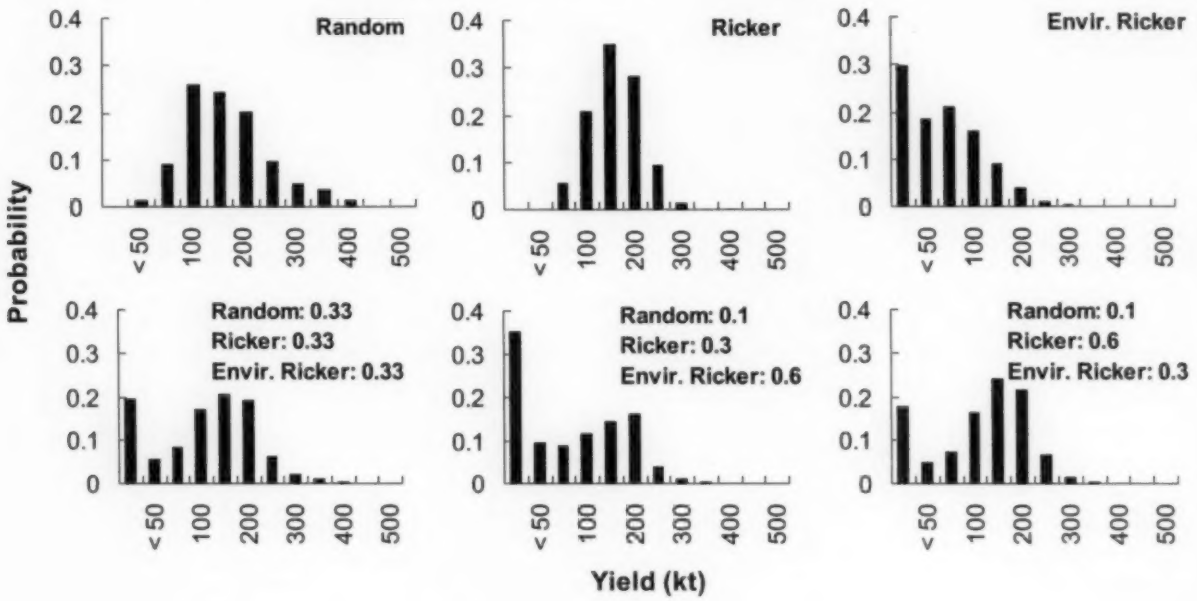

Table 7. Expected utilities (values of objective function) at different effort levels for the two mesh sizes.

	Gill net *F* factor				
Trawl *F* factor	1.3	1	0.8	0.5	0.2
Mesh size: 120 mm					
1.3	<u>76</u>	84	88	98	110
1	102	122	122	135	146
0.8	126	137	147	161	173
0.5	162	168	173	177	**178**
0.2	151	147	141	129	116
Mesh size: 140 mm					
1.3	141	139	147	162	176
1	148	160	167	183	193
0.8	165	176	183	192	**201**
0.5	176	181	183	185	182
0.2	150	146	136	127	<u>111</u>

Note: Utilities are defined in the text and in Table 5. The highest value is in bold and the lowest is underlined. Effort: 1 = present value, 0.8 = 0.8 × present value, etc.

Table 8. Expected catches (kt) at different effort levels for the two mesh sizes.

	Gillnet *F* factor				
Trawl *F* factor	1.3	1	0.8	0.5	0.2
Mesh size: 120 mm					
1.3	<u>91</u>	100	104	114	125
1	119	140	137	150	159
0.8	140	152	161	173	**183**
0.5	171	175	180	182	181
0.2	154	148	141	129	116
Mesh size: 140 mm					
1.3	162	154	162	176	190
1	164	175	180	194	201
0.8	179	187	193	199	**206**
0.5	183	186	188	187	183
0.2	152	148	137	127	<u>111</u>

Note: The highest value is in bold and the lowest is underlined. *F* factor: 1 = present value, 0.8 = 0.8 × present value, etc.

the use of the other S/R models, in which the positive effect of high biomass on recruitment is taken into account.

However, the more one takes the positive feedback of the spawning stock into account, the less one should fish (moving down or right from the upper left corner). As belief in the environmental Ricker model grows, the advice becomes increasingly conservative; reduced fishing mortality rates are advised for both gear types. Recommendations to reduce effort would be stronger for the 120-mm mesh size than for the 140-mm mesh size (Figs. 4 and 5). In other words, when the risk of oxygen deficiency in the spawning areas is taken into account, the spawning stock must be kept at a higher level to create a buffer against long periods of poor recruitment. During the infrequent periods of good spawning conditions, a sufficiently large spawning stock biomass must be present to produce a strong year-class.

With the 140-mm mesh size and a strong belief in the Ricker or random model the advice would be to increase the fishing mortality rate of trawls. Intensive fishing with a

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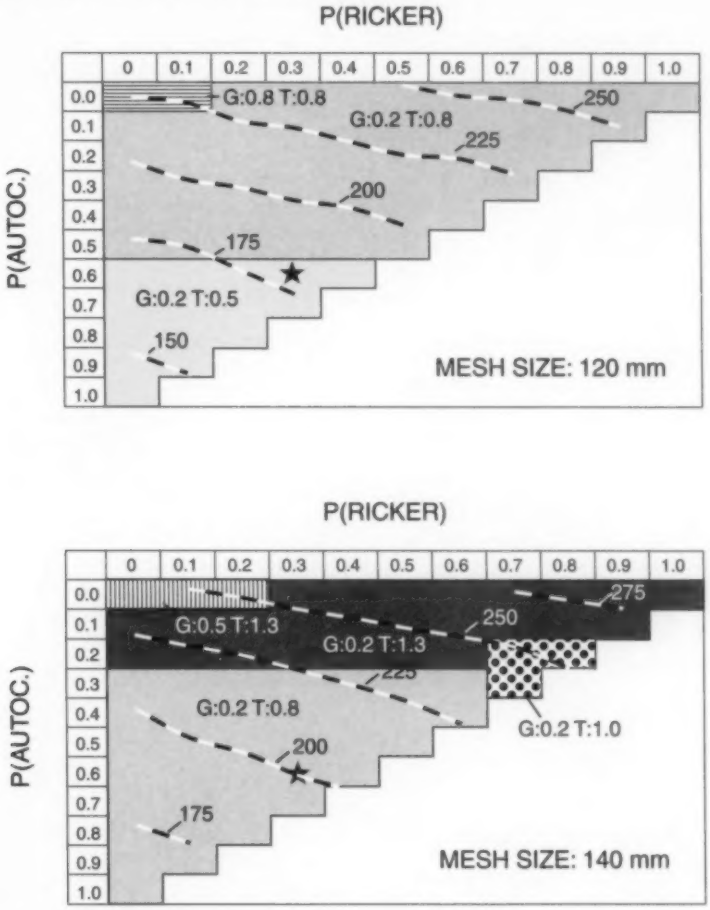
Fig. 4. Sensitivity of the optimal decisions to the prior probabilities of different recruitment models for two mesh sizes. The columns show the probabilities given to the Ricker model and the rows the probabilities given to the environmental Ricker model. The remaining probability = $1 - (P_{column} + P_{row})$ was given to the random model. The patterns show areas of different optimal decision combinations. The optimal fishing mortalities are given in discrete classes for the different gear types (G, gillnet *F* factor; T, trawl *F* factor). The *F* factors indicate change relative to present fishing mortality rates, e.g., 0.2 = 20% of present *F*. The lines describe the levels of expected utility for the optimal decision. The catch and the biological risk determine the utilities. The assumed combination of prior probabilities is indicated by a star. See text for additional explanation.



wide-meshed trawl would allow efficient exploitation of the growth potential of cod and at the same time somewhat counter the negative effects of cannibalism.

Note that the preferred exploitation levels are more sensitive to probabilities when a smaller mesh size is used (Figs. 4 and 5). The same is apparent if we examine the value of information for the two mesh sizes (Table 9). These show that the value of information for all variables (recruitment process is the key uncertainty) is about 7% of total utility for the 120-mm mesh size and that it decreases significantly when a 140-mm mesh size is used. Thus, with a larger mesh size, preferred exploitation levels become less sensitive to assumptions about future recruitment and growth levels and the monitoring of fishing mortalities. Moreover, the implementation uncertainty of fishing mortality would not be as remarkable as in the case of the smaller mesh size.

Discussion

Dealing with uncertainty

From a strictly decision-making point of view, the only uncertainties that matter are those capable of changing the decision at hand. The significance of different sources of scientific information depends, however, on the type of management decisions being considered. For example, our focus on intermediate- and long-term strategic decisions meant that additional knowledge of growth rate had no informational value, although growth rate is a key variable in short-term catch predictions (Table 9). The need for knowledge is related both to the management objectives and to the possibilities for controlling the system.

A potential problem with using approaches dealing with uncertainties is that managers may get the impression that "all" relevant uncertainties have been addressed. We focused

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Fig. 5. Same as Fig. 4, but with catch as the only objective. The lines give directly the expected catches of optimal decisions.

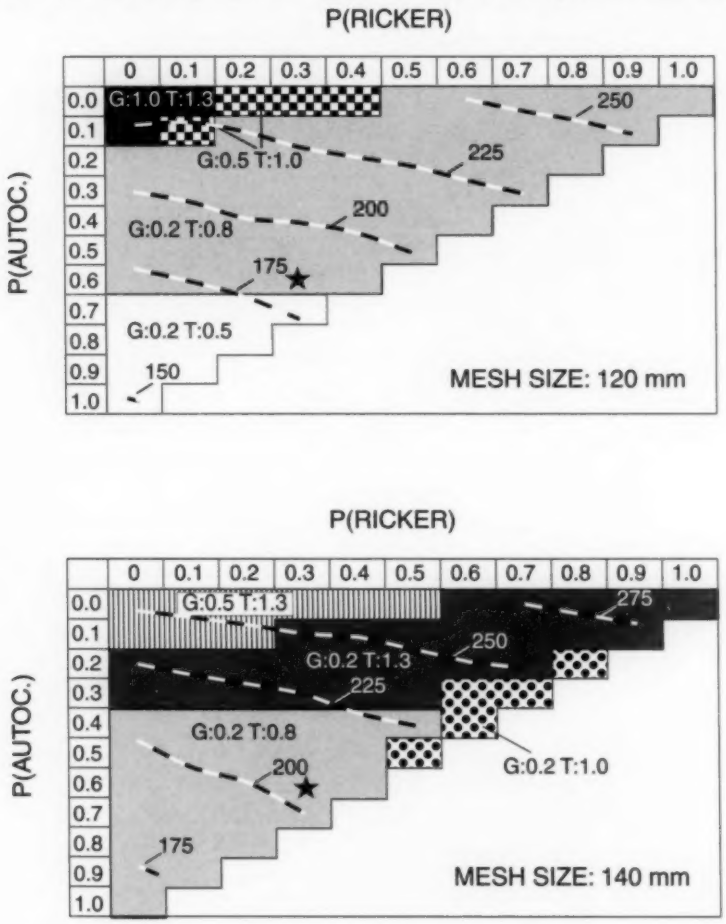

Table 9. Value of perfect information (in units of utility function) for different prior variables in a case when either 120- or 140-mm mesh size is used in the fishery.

Prior variable	Mesh size: 120 mm	Mesh size: 140 mm
Recruitment process	11.7	5.8
Growth	0.04	0.0
Biomass criteria	0.0	0.0
All variables	12.9	7.6

on the effects of recruitment uncertainties on management decisions, but there are obviously other sources of uncertainty, too, such as variations in the natural mortality rates, the level of cannibalism, and the survival of trawl escapees, that could affect the results of management decisions. For example, cannibalism could increase at low fishing mortality rates more than we have assumed, thereby further depressing recruitment to the fishable stock. Moreover, there are indications that the survival of trawl escapees is not 100% as we have assumed (Suuronen et al. 1996; Finnish Game and Fisheries Research Institute, unpublished data). Underestimation of uncertainties leads to overestimation of the system's controllability. As a result, managers receive too optimistic a perception of the feasibility of reaching the desired state of the system.

The approach in our analysis deals with uncertainties related to growth and recruitment. Our choice was based on the assumption that the intermediate management strategies for Baltic cod could require new mesh size rules. Strategic changes of such a nature stress the importance of realistic selection modeling (Myers 1989). Our approach using selection curves and the modeling of length distributions was a response to this requirement.

Our findings suggest increasing gains with reduced fishing mortality rates for Baltic cod. In theory, this effect could be offset by density-dependent effects that retard growth. Myers and Cadigan (1993), for example, showed that neglect of density dependency easily leads to flawed conclusions. Our model was not designed to analyze the effect of this hypothesis. To do that, dependency should be included in the Monte Carlo simulation model to enable the effects of size on the age- and gear-specific fishing mortalities to be modeled.

Our assumptions of Baltic cod recruitment cover a wide

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range of possible recruitment processes. However, we excluded considerations of species interactions, although evidence exists that the SPVOL and the sprat stock may interact to produce the observed cod recruitment (Sparholt 1996). A likely effect would have been further depression of cod recruitment at high fishing mortalities. Low fishing mortalities of cod might have had the reverse effect, as a large cod stock with big individuals would be able to depress the sprat stock. Therefore, our results are probably conservative with respect to the effects of the fishing mortality rates of cod.

In addition to the uncertainties related to the ecological system, there are uncertainties related to the management objectives. Due to political changes in the use of natural resources, objectives may change in the future, as well. An example is the inclusion or exclusion of recruitment risk. In the case of smaller mesh size, the weight given to recruitment risks affects the decision only if S/R knowledge is not included in the model (compare upper right corner of 120-mm mesh size in Figs. 4 and 5). If a separate risk indicator is used, the information on weighting should be obtained from responsible managers. An advantage of using utilities rather than catch alone is the possibility of dealing explicitly with different weights. It is conceptually easy to introduce other management interests in the utility calculation, but in practice, it is difficult to estimate the objective functions of various interest groups. In such a case, a decision analyzer can examine several alternative objective functions and show which assumptions really matter.

Other major uncertainties not included in our models are related to implementation of the management measures. Uncertainty about stock size is a major issue in all TAC-based management systems. Cod migration between sea areas or the existence of substocks could affect, for instance, the benefits of a mesh size change. Trawlers may also respond to new regulations by adopting practices that circumvent these regulations. The short-term losses due to an increase in trawl mesh size to 140 mm would be considerable and could lead to the use of herring trawls in cod fishing, with serious discarding problems. The role of the gillnet fishery should be studied in greater detail than hitherto. The gillnet mesh size (105 mm) that we used in our analysis is the minimum allowed, but the mesh size of most of the nets used on the Swedish coast, for instance, is >105 mm (Tschernij and Koppetch 1997). These practical problems should also be considered in the actual decision-making, as they might offset the expected gains of a larger mesh size.

Uncertainty and the sustainability of the fishery

An important consideration in dealing with uncertainty is the extent to which perception of the state of a fish stock changes relative to a deterministic analysis. In the first modeling step, the simple Y/R calculation showed that changes in fishing mortality and in mesh size would be profitable. Taking the uncertain information on an S/R relationship and the effects of environmental factors into account in the second step supported this conclusion and made the change look even more profitable. A deterministic analysis would have led to qualitatively similar conclusions. However, point estimate models do not deal so effectively with information quality and system controllability. Influence diagram models make a discussion of risk assessment and risk management (Pearse and Walters 1992) meaningful by allowing us to examine the present management scheme in relation to various risks in an uncomplicated way. Uncertain and subjective information, which is difficult to justify in a deterministic analysis, can be used and tested effectively. In our case the environmental Ricker model demonstrates the importance of such information.

The environmental Ricker model gave a pessimistic view of the possibilities of the stock to sustain present fishing mortality rates. The high probability of low yield and biomass in the case of high fishing mortality is based on short-term trends in water quality and on the assumption that the environmental quality would decline further. While future changes in water quality in the Baltic Sea are uncertain, trends in nutrient loads and changes in hydrographic conditions (Möller and Hansen 1994) suggest a marked decline in water quality.

The simulation results obtained with the environmental Ricker model conflict with those from the other models, thus reducing the information content of the combined estimates (Fig. 3, lower panel). The probability distributions are generally wide, indicating poor predictability at present fishing mortality rates. Lower fishing mortality rates lead to narrower distributions, indicating better controllability and predictability.

Our overall assessment supports earlier findings that the current Baltic cod fishery is not sustainable (e.g., Anonymous 1997; Hildén 1997*c*). By this, we mean that at the present fishing mortality rate, there is a fairly high probability of a substantial decrease in biomass and yield. The medium-term projections in Anonymous (1996) did not include autocorrelated environmental factors, which clearly lead to underestimation of the risk of a stock collapse. Our observation is not new; Engen et al. (1997), for example, showed that the optimal threshold for harvesting declines with environmental variance. Use of historical data, as in the analysis of Anonymous (1996), implicitly assumes that water quality will not deteriorate in the future. However, advice is given for the future and the exploitation rate should be designed with future uncertainties in mind.

Implications for Baltic cod fisheries management

A key finding of our study is that assumptions of environmental variability make a significant difference to conclusions regarding fisheries management. A combination of declining trends in water quality and high exploitation level is dangerous for stock and fishery alike. More age-classes are needed to provide a buffer against environmentally poor years with poor recruitment. With a sufficient buffer stock, the fishery could be allowed to retain the levels of catches after poor recruitment years. If the fishery is, as at present, heavily dependent on recruitment, fishers and managers must be ready to adjust the TAC at short notice after a prediction of poor recruitment. Historically, Baltic fisheries managers have not been willing to cut TAC's substantially to regulate the fishery. The International Baltic Sea Fishery Commission has agreed on TAC levels that have been above actual catches, despite high fishing mortality rates (Anonymous 1997). Our estimates suggest that, with better management, the mean yearly catch could be increased by 66 000 t.

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This would be a remarkable improvement when compared with recent yearly catches.

The study of uncertainties provides additional arguments in favor of increasing the minimum mesh size in the Baltic cod fishery. It shows that there would then be less need to use TAC as a strong regulative instrument. Increasing mesh size to 140 mm would markedly reduce the frequency of dangerously low spawning biomasses and the need for very low TAC's.

The finding that a larger mesh size is beneficial irrespective of the assumed recruitment process is also important, as it implies that the key conclusions remain valid despite considerable uncertainty concerning the future state of the environment. The robustness of the conclusions is important in management negotiations, which can be expected to raise many doubts about the wisdom of making radical changes to the status quo.

We have focused only on management strategies related to fishing mortality rates and mesh size in the face of environmental uncertainties. There are other possible strategies that could effectively support the objectives of all fisheries stakeholders. Sparholt (1995) suggested keeping the spawning stock biomass at a level of 0.5–0.6 million t, which would give maximum sustainable yield under a broad range of environmental conditions. Our analysis strongly suggests that under present and foreseeable environmental conditions, such goals could be achieved only by reducing fishing mortality rates. Our findings also agree with those of Horbowy (1995). Using Monte Carlo simulations, he showed that long-term catch levels could be increased substantially by reducing fishing mortality rates.

An important finding in influence diagram modeling is the sensitivity of the value of information to the management context. The difference in the value of information between the 120- and 140-mm mesh size (Table 9) can be explained by the changing role of the fishing mortality rate. Expected utilities are much more sensitive to changes in F at 120- than at 140-mm mesh size (Tables 7 and 8). Correct stock assessment and implementation of TAC management are therefore less important at the 140-mm mesh size than they are at the 120-mm mesh size (also see Myers and Mertz 1998).

Differences in the value of information between different management regimes have far-reaching consequences. For example, knowledge about the recruitment process is generally considered one of the keys to successful management of fish stocks (Rotschild 1986). Our study shows that the role of this knowledge can be diminished simply by shifting the management strategy, in our case, by increasing the mesh size. Such a measure would not remove all uncertainties, but it would act as an "insurance fee" against their negative impacts. In the Baltic Sea cod fishery, this fee would be the short-term catch loss after a mesh size change. Decision analysis can thus identify management strategies that are less sensitive to scientific uncertainty and implementation errors. Metamodeling of structural uncertainties using Bayesian influence diagrams can be an efficient tool in the search for robust strategies of this nature.

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2,2′,4,4′,5,5′- and 3,3′,4,4′,5,5′-Hexachlorobiphenyl pretreatments alter the biliary excretion of a challenge dose of 7,12-[^{3}H]dimethylbenz[*a*]anthracene in rainbow trout (*Oncorhyncus mykiss*)

Eugene P. Foster and Lawrence R. Curtis

Abstract: This study compared disposition of a polycyclic aromatic hydrocarbon (PAH) in rainbow trout after di-ortho and non-ortho polychlorinated biphenyl (PCH) pretreatments. Four weeks after intraperitoneal (i.p.) injection with 50 or 250 μg of the di-ortho 2,2′,4,4′,5,5′-hexachlorobiphenyl (2HxCB)·g^{-1} or 5 or 25 μg of the non-ortho 3,3′,4,4′,5,5′-hexachlorobiphenyl (3HxCB)·g^{-1}, rainbow trout were i.p. injected with 10 nmol [^{3}H]7,12-dimethylbenz[*a*]anthracene (DMBA)·g^{-1}. Livers and gallbladders were removed 16 h later. Biliary excretion of [^{3}H]DMBA decreased after i.p. injection of 2HxCB or 3HxCB. In a second experiment, rainbow trout were fed 60 or 220 ng 2HxCB·g fish^{-1}·day^{-1} or 1.9 or 7.8 ng 3HxCB·g fish^{-1}·day^{-1} for 4, 8, or 12 weeks. Fish were then i.p. injected with 10 nmol [^{3}H]DMBA·g fish^{-1}. Liver, bile, mesenteric fat, stomach, muscle, kidney, and plasma were sampled 16 h later. Fish fed 220 ng 2HxCB·g fish^{-1}·day^{-1} for 4 weeks and 60 or 220 ng 2HxCB·g fish^{-1}·day^{-1} for 8 weeks had greater biliary concentrations of [^{3}H]DMBA than controls. Biliary [^{3}H]DMBA increased for fish fed 7.8 ng 3HxCB·g fish^{-1}·day^{-1} for 4 weeks. Thus, feeding both di-ortho and non-ortho PCBs transiently stimulated [^{3}H]DMBA biliary excretion. Growth and survival data indicated no overt toxicity of the PCB doses used here via either exposure route. High i.p. doses that inhibited biliary excretion of [^{3}H]DMBA were probably less environmentally relevant than the dietary doses fed here.

Résumé : Notre étude compare l'élimination d'un hydrocarbure aromatique polycyclique (HAP) chez la truite arc-en-ciel après des pré-traitements avec des di-ortho et non-ortho-polychlorobiphényles (PCB). Quatre semaines après l'injection intrapéritonéale de 50 ou 250 μg de di-ortho-2,2′,4,4′,5,5′-hexachlorobiphényle (2HxCB)·g^{-1}, ou de 5 ou 25 μg de non-ortho-3,3′,4,4′,5,5′-hexachlorobiphényle (3HxCB)·g^{-1}, on a injecté aux truites arc-en-ciel 10 nmol [^{3}H]7,12-diméthylbenz[a]anthracène (DMBA)·g^{-1}. Les foies et les vésicules biliaires ont été prélevés 16 h plus tard. L'excrétion biliaire de [^{3}H]DMBA a baissé après l'injection intrapéritonéale de 2HxCB ou de 3HxCB. Dans une deuxième expérience, on a administré à des truites arc-en-ciel dans la nourriture 60 ou 220 ng de 2HxCB·g poisson^{-1}·jour^{-1}, ou 1,9 ou 7,8 ng de 3HxCB·g poisson^{-1}·jour^{-1}, pendant 4, 8 ou 12 semaines. On a ensuite injecté aux poissons par voie intrapéritonéale 10 nmol [^{3}H]DMBA·g^{-1}. Seize heures plus tard, on a échantillonné le foie, la bile, la graisse mésentérique, l'estomac, le muscle, le rein et le plasma. Les poissons qui avaient reçu 220 ng de 2HxCB·g poisson^{-1}·jour^{-1} pendant 4 semaines et 60 ou 220 ng de 2HxCB·g poisson^{-1}·jour^{-1} pendant 8 semaines présentaient des concentrations biliaires de [^{3}H]DMBA supérieures à celles des témoins; ces concentrations avaient augmenté chez les poissons qui avaient reçu 7,8 ng de 3HxCB·g poisson^{-1}·jour^{-1} pendant 4 semaines. L'administration de di-ortho et non-ortho-PCB a donc stimulé de façon temporaire l'excrétion biliaire de [^{3}H]DMBA. Les données sur la croissance et la survie n'ont pas fait ressortir de toxicité évidente pour les doses de PCB employés ici par l'une ou l'autre voie d'exposition. Les fortes doses injectées par voie péritonéale qui inhibaient l'excrétion biliaire de [^{3}H]DMBA étaient probablement moins pertinentes sur le plan environnemental que les doses reçues ici dans l'alimentation.

[Traduit par la Rédaction]

Introduction

Fish and other aquatic life are not exposed to single chemicals in natural waters but to complex mixtures. Polycyclic aromatic hydrocarbons (PAHs) and polychlorinated biphenyls (PCBs) are two classes of environmental contaminants that co-occur in the aquatic environment because similar physical and chemical characteristics determine their fate

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and transport. Both classes of chemicals are hydrophobic, lipophilic, resistant to biological and chemical degradation, and toxic. The predominant fate of PAHs and PCBs in aquatic systems is deposition to the sediments where they are available for uptake by benthic organisms and trophic transfer to fish and other aquatic life.

Toxic interactions of complex mixtures of PAHs and PCBs are incompletely characterized, whereas individual chemical and congener toxicity are better understood. The toxic potency for many PAHs and PCBs that have a planar conformation is associated with interaction with the arylhydrocarbon receptor (AhR), a ligand-activated transcription factor (reviewed in Safe 1990). Expression of cytochrome P4501A (CYP1A) genes increases after AhR activation. Increases in tissue CYP1A proteins indicate exposure of fish to chlorinated dioxins and furans, planar PCBs (van der Weiden et al. 1994), PAHs, or other compounds that bind the AhR. Stimulation of CYP1A-mediated enzymatic activities such as arylhydrocarbon hydroxylase (AHH) and exthoxyresorufin-*O*-deethylase (EROD) are common measures for AhR activation (Safe 1990).

PAHs were carcinogenic in laboratory fish (Fong et al. 1993) and PAHs in sediments were associated with incidence of hepatic tumors in wild fish (Malins et al. 1985). The classic PAH carcinogenesis model involves metabolism of parent PAH to a reactive intermediate that covalently binds to DNA forming adducts that can lead to mutations and eventual neoplasia. 7,12-Dimethylbenz[*a*]anthracene (DMBA), which was detected in estuarine sediments (Bieri et al. 1986), was a weak carcinogen that was metabolized by CYP1A and epoxide hydrolase systems to a potent carcinogenic diol 3,4-dihydrodiol dimethylbenz[*a*]anthracene (DiGiovanni et al. 1983) found in the bile of rainbow trout treated with DMBA (Schnitz et al. 1993).

Prevalence of PCBs in environmental samples and toxicity varies between individual congeners. The di-ortho, nonplanar congener, 2,2′,4,4′,5,5′-hexachlorobiphenyl (2HxCB) (IUPAC 153) was detected most frequently, whereas the non-ortho planar congener 3,3′,4,4′,5,5′-hexachlorobiphenyl (3HxCB) (IUPAC 169) was rarely detected in environmental samples. However, di-ortho PCBs are less toxic than the non-ortho PCBs. Planar PCBs like 3HxCB activate the AhR (Safe 1990) and increase rainbow trout CYP1A mRNA and protein in a dose-dependant manner (Donohoe et al. 1995). 2HxCB exhibited low biological activity and toxicity, which was attributed to negligible AhR affinity because of nonplanar conformation (Safe 1990). Low AhR affinity was supported by absence of induction of EROD and CYP1A in fish exposed for short durations to 2HxCB (van der Weiden et al. 1994). However, longer exposure of fish to 2HxCB increased AHH and EROD activities (da Costa and Curtis 1995) associated with induction of CYP1A mRNA and protein (Foster et al. 1998).

PCB induction of CYP1A could increase PAH metabolism, affecting disposition and ultimate toxicity by increasing metabolism of PAH to toxic metabolites. Pretreatment with commercial mixtures of PCBs or PAHs altered PAH metabolite formation (Tan et al. 1981; Swain and Melius 1984). However, the effects of individual PCB congeners on PAH disposition have not been well investigated in fish. This work assessed the in vivo interaction of a PAH with di-ortho or non-ortho persistent PCB congeners known to induce hepatic CYP1A in fish. Specifically, it compared the effects of pretreatments with 2HxCB or 3HxCB on the disposition of [^{3}H]DMBA in rainbow trout.

Methods

Experimental animals

Juvenile Shasta strain rainbow trout (15–60 g) were obtained from the Food Toxicology and Nutrition Laboratory, Oregon State University. Two fish that received the same pretreatment dose of PCB were kept in aerated glass aquaria (61 × 32 × 20 cm; 23 L total volume), separated by a partition, and received a continuous flow of well water (100 mL/min at 14 ± 2°C). Fish administered the PCB in food were fed a 5% body weight (dry weight fish/dry weight diet) ration of Oregon Test Diet (OTD) (Lee at al. 1991) per day given as three feedings per week. Fish i.p. injected with PCBs were fed a 3% body weight (dry weight fish/dry weight diet) ration of OTD per day given as three feedings per week. Fish weights were measured every 4 weeks for fish fed PCBs and weekly for i.p.-injected fish with rations adjusted accordingly. Tank debris was removed 3 times weekly. A 12:12 h light:dark cycle was maintained throughout the study. Specific growth rate was calculated as

$$(\mathrm{Ln}W_2 - \mathrm{Ln}W_1) / (t_2 - t_1) \times 100.$$

Chemicals

Fish were treated with 2HxCB (IUPAC 153) (Accustandard, New Haven, Conn.) that was >99% pure and had <1% total mono–ortho PCBs detected by gas chromatography–mass spectrometry (da Costa and Curtis 1995). No other PCBs, chlorinated dioxins, or dibenzofurans were detected. 3HxCB (IUPAC 169) (Accustandard, New Haven, Conn.) purity was >99%. [^{3}H]DMBA (Amersham Corp., Arlington Heights, Ill.) (specific activity 63 Ci/mmol (1 Ci = 37 GBq)) and DMBA (Aldrich Chemical Co., Milwaukee, Wisc.) cleanup were performed according to DePierre et al. (1975). Briefly, DMBA cleanup was performed by adding 2 mL of 0.25 N NaOH with 40% ethanol to 4 mL of hexane with [^{3}H]DMBA and DMBA. The mixture was vortexed for 1 min and then centrifuged at 2000 rpm for 5 min. NaOH–ethanol was removed and NaOH–ethanol was added, vortexed, centrifuged, and removed two more times as stated above. After final removal of NaOH–EtOH, the hexane was evaporated with N_2 and acetone was added. [^{3}H]DMBA/DMBA purity was analyzed by HPLC after cleanup and no metabolite peaks were observed.

[^{3}H]DMBA time course

Fish were i.p. injected with 10 nmol [^{3}H]DMBA·g fish^{-1} in rock fish oil (5 mL/kg) and 4, 8, 16, 18, and 32 h later bile (gallbladder + bile), liver, mesenteric fat, kidney, plasma, and stomach were sampled. Whole tissue or subsamples of 4:1 water:tissue homogenates were solubilized in Soluene 350 (Packard, Downers Grove, Ill.) and [^{3}H]DMBA was measured using a Packard 1600CA Tri-Carb liquid scintillation analyzer and Ultima Gold scintillation cocktail (Packard, Downers Grove, Ill.).

[^{3}H]DMBA disposition after PCB pretreatment

Fish were given a single i.p. injection of 50 or 250 µg 2HxCB·g^{-1} or 5 or 25 µg 3HxCB·g^{-1} in corn oil (5 mL/kg) and were sampled 4 weeks later. Controls received corn oil only. In another experiment, fish were fed a diet of 0, 6, or 220 ng 2HxCB·g fish^{-1}·day^{-1} (calculated cumulative 12-week doses of 1.68 and 6.160 µg 2HxCB·g fish^{-1}) and 2 or 8 ng 3HxCB·g fish^{-1}·day^{-1} (calculated cumulative 12-week doses or 0.056 and 0.224 µg 3HxCB·g fish^{-1}) administered three times per week for 4, 8, and 12 weeks. Following PCB treatment, fish were i.p. injected with 10 nmol

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Table 1. Specific growth rate and liver-somatic index for fish injected i.p. with 50 or 250 μg 2HxCB·g fish^{-1} or 5 or 25 μg 3HxCB·g fish^{-1} 4 weeks earlier.

		2HxCB μg·g^{-1}		3HxCB μg·g^{-1}	
	Control	50	250	5	25
Growth	1.03	1.01	0.93	0.98	0.94
	(0.04)	(0.05)	(0.03)	(0.09)	(0.09)
LSI	0.67	0.69	0.79*	0.80*	0.90*
	(0.02)	(0.02)	(0.05)	(0.03)	(0.07)

Note: Specific growth rates are means (SEM) for $n = 6$ (mg·g fish^{-1}·day^{-1}). LSI, liver-somatic index (liver weight to body weight ratio), $n = 6$ (SE).
*Significantly different from controls ($p < 0.05$).

Table 2. Liver-somatic index and specific growth rate for fish fed 2HxCB or 3HxCB for 4, 8, or 12weeks.

	LSI			Growth		
	Week 4	Week 8	Week 12	Week 4	Week 8	Week 12
Control	1.03	1.14	1.13	0.80	0.74	0.76
	(0.13)	(0.05)	(0.06)	(0.04)	(0.02)	(0.04)
2HxCB						
60 ng·g^{-1}·day^{-1}	0.74	0.72	0.64	1.28	1.19	1.32
	(0.20)	(0.02)	(0.05)	(0.07)	(0.06)	(0.08)
220 ng·g^{-1}·day^{-1}	0.833	0.68	0.73	0.93	1.06	1.16
	(0.06)	(0.06)	(0.05)	(0.08)	(0.04)	(0.10)
3HxCB						
2 ng·g^{-1}·day^{-1}	0.92	0.84^{a,b}	0.74^{b}	1.30	1.27	1.14
	(0.03)	(0.04)	(0.02)	(0.06)	(0.05)	(0.02)
8 ng·g^{-1}·day^{-1}	0.92	0.95^{b}	0.79^{a,b}	1.78	1.26	1.18
	(0.06)	(0.05)	(0.02)	(0.38)	(0.04)	(0.03)

Note: Controls were calculated as a grand mean for both experiments. Control LSI values are the mean (SEM) for $n = 4$ at 4 weeks and $n = 8$ at 8 and 12 weeks. The LSI values for 2HxCB and 3HxCB treated fish are $n = 4$ at each time. Specific growth rates for controls were calculated from $n = 24$, 16, and 8 at 4, 8, and 12 weeks, respectively. Growth rates for 2HxCB and 3HxCB treatments were calculated for $n = 12$ (SE) for week 4, $n = 8$ (SE) for week 8, and $n = 4$ (SE) for week 4. Dissimilar letter denotes treatment difference.

[^{3}H]DMBA·g^{-1} in rock fish oil and sampled 16 h later. Bile (gallbladder + bile), liver, mesenteric fat, stomach, skeletal muscle, kidney, and plasma were sampled from fish fed PCBs and bile (gallbladder + bile) and liver were sampled from PCB i.p. injected fish. Tissues were prepared and analyzed for [^{3}H]DMBA as described above.

Data analysis

Percentage data were arscine transformed prior to statistical analyses. Data were screened for presence of outliers with the Dixon Test ($p < 0.01$). There was no difference between time points for feeding study controls (one-way analysis of variance), which were then pooled for identifying treatment effects. Differences between treatments were detected using one-way analysis of variance and the least significant difference (LSD) multiple comparison test (one-tailed $p < 0.05$) unless otherwise specified.

Results

Overt toxicity

The liver-somatic index (LSI) increased in fish i.p. injected with the high dose of 2HxCB and both doses of 3HxCB (Table 1). LSI increased in fish fed 8 ng 3HxCB·g fish^{-1}·day^{-1} for 8 weeks and decreased after 2 ng 3HxCB·g fish^{-1}·day^{-1} for 12 weeks (Table 2). There was no change in LSI for 2HxCB fed fish. There was no treatment effect of i.p. 2HxCB or 3HxCB on specific growth rate (Table 1). Specific growth rate of fish fed 8 ng 3HxCB·g fish^{-1}·day^{-1} was higher after 4, but not 8 or 12, weeks of treatment. Specific growth rates of 2HxCB-fed fish were not significantly different than control.

[^{3}H]DMBA diposition in bile and liver

Dispositon of [^{3}H]DMBA to bile and liver of control rainbow trout increased with time (Fig. 1). At 32 h after injection, the bile and liver contained less than 3.0% and 0.7% of the [^{3}H]DMBA administered dose, respectively. Regression analysis expressed tissue [^{3}H]DMBA as a function of time. There was a significant positive correlation between [^{3}H]DMBA equivalents and time for bile 4 to 32 h and for liver 8 to 32 h after i.p. injection (Fig. 1). Kidney, mesenteric fat, plasma, and stomach [^{3}H]DMBA equivalents were not correlated with time (data not shown).

PCBs altered [^{3}H]DMBA diposition in bile and liver

Biliary [^{3}H]DMBA equivalents (nmol·g bile^{-1}) decreased in fish that were i.p. injected with 2HxCB and 3HxCB 4 weeks prior to the challenge dose of the PAH (Table 3). The mean biliary [^{3}H]DMBA (% dose·mg^{-1}) for fish fed 220 ng 2HxCB·g fish^{-1}·day^{-1} for 4 weeks was approximately 3 times greater than controls. In fish fed 60 and 220 ng 2HxCB·g fish^{-1}·day^{-1} for 8 weeks, biliary [^{3}H]DMBA contents were approximately 1.5 times greater than controls

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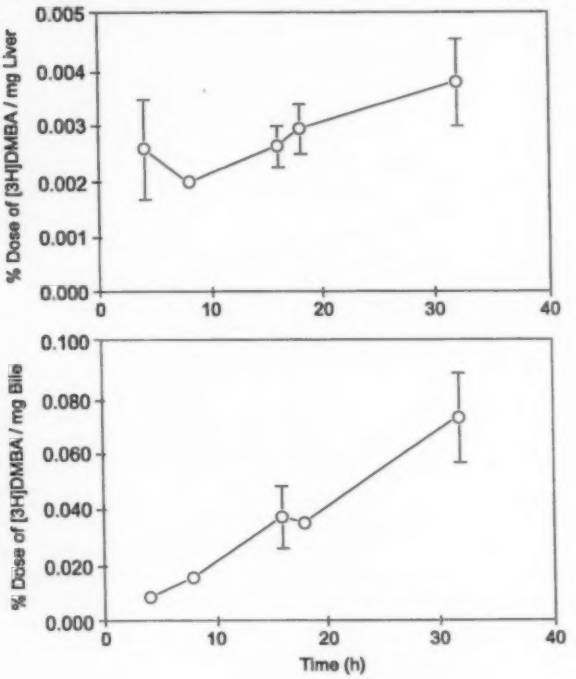
Fig. 1. Mean biliary and liver [^{3}H]DMBA equivalents as % dose·g tissue^{-1} 4 to 32 h after i.p. injection with 10 nmol [^{3}H]DMBA·g fish^{-1}. Error bars are standard error. n = 4 for each time point. Regression equations: % dose·g bile^{-1} = 4.25 + 14.75x, p-value < 0.0001, adjusted r^2 = 62.7; % dose·g liver^{-1} = 2.13 + 0.34x, p-value < 0.079, adjusted r^2 = 16.1; 8- to 32-h time point % dose·g liver^{-1} = 1.49 + 0.07x, p-value < 0.014, adjusted r^2 = 35.8.



(Fig. 2). Mean hepatic [^{3}H]DMBA (% dose·mg^{-1}) approximately doubled in fish fed 220 ng 2HxCB·g fish^{-1}·day^{-1} for 4 weeks (Fig. 2). Biliary [^{3}H]DMBA (% dose·mg^{-1}) increased in fish fed 8 ng 3HxCB·g fish^{-1}·day^{-1} for 4 weeks with no change in liver (Fig. 3). There were no changes in kidney, mesenteric fat, plasma, stomach, or muscle [^{3}H]DMBA equivalents with any PCB treatment (data not shown).

Discussion

Fish are exposed to complex mixtures of environmental pollutants. Persistent contaminants such as chlorinated dioxins and furans, PCBs, and PAHs occur in aquatic bed sediments and fish tissues, confirming exposure to complex mixtures of these agents. The biological interactions of complex mixtures of contaminants are important because of the potential for altered xenobiotic disposition and toxicity.

Recent work focused on the additivity of responses for compounds with toxicities mediated by the AhR. Induction of CYP1A by non-ortho, planar PCBs was well documented in fish (Zabel et al. 1995). Evidence for interaction of the di-ortho, nonplanar 2HxCB with CYP1A was only recently reported (da Costa and Curtis 1995; Foster et al. 1998). This study examined the disposition of [^{3}H]DMBA in rainbow trout following pretreatments with 2HxCB or 3HxCB. Two pretreatment regimens were tested. (*i*) High PCB doses were administered by i.p. injections and [^{3}H]DMBA disposition was examined 4 weeks later. Specific growth rates indicated no overt toxicity of these pertreatments (Table 1). (*ii*) Fish were fed PCB doses (ng·g^{-1}·day^{-1}) over 12 weeks and [^{3}H]DMBA dispositon was examined over time. As anticipated from results of i.p. injections with high doses, specific growth rates suggested no overt toxicity of the dietary PCB pretreatments (Table 2).

Disposition of [^{3}H]DMBA to liver and bile increased with time up to 32 h after i.p. injection (Fig. 1, Table 3). The [^{3}H]DMBA dose used in this study resulted in environmentally relevant PAH concentrations in the liver. [^{3}H]DMBA equivalents in liver and bile were approximately an order of magnitude higher than those found in brown trout (*Salmo trutta*) and white sucker (*Catastomus commersoni*) and approximately two orders of magnitude lower than phenanthrene muscle tissue levels for lamprey (*Petromyzon marinus*) collected from the Hershey River (McElroy et al. 1989). In addition, liver and bile [^{3}H]DMBA equivalents after i.p. injection were comparable (1 and 2%, respectively, after 16 h) to results reported for fish orally exposed to DMBA (O'Connor et al. 1988; Schnitz et al. 1987). DMBA appears to be more slowly excreted than benzo[*a*]pyrene in rainbow trout. The mean [^{3}H]DMBA biliary concentration 32 h after i.p. injection was 124 nmol·g^{-1} (Fig. 1), whereas bile from fish i.p. injected with 10 nmol [^{3}H]benzo[*a*]pyrene·g^{-1} and then sampled 24 h later had approximately 700 nmol [^{3}H]benzo[*a*]pyrene·g^{-1} (Curtis et al. 1990).

Xenobiotic pretreatment can stimulate hepatic metabolism, altering the biliary metabolite profile and increasing production of toxic metabolites. Aroclor 1254 treatment of mullet increased the production of 9,10-dihydro-9,10-dihydroxybenzo[*a*]pyrene, 4,5-dihydro-4,5,-dihydroxybenzo[*a*]pyrene, 7,8-dihydro-7,8-dihydroxybenzo[*a*]pyrene, and unidentified quinones in the hepatic S9 fraction incubated with benzo[*a*]pyrene (Tan et al. 1981). The carcinogenic metabolite 3,4-dihydrodiol dimethylbenz[*a*]anthracene was identified in the bile after multiple doses and 2-hydroxy-DMBA and 3-hydroxy-DMBA were identified following a single dose of DMBA to rainbow trout (Schnitz et al. 1993).

CYP1A was identified as the primary oxidative enzyme family in metabolism of PAHs in fish. Studies that were run side-by-side with the work reported here showed that EROD activities and CYP1A protein increased in a dose–response fashion for rainbow trout exposed i.p. to 2HxCB (Foster et al. 1998); however, there was inhibition from i.p. injected 3HxCB at the higher dose with a significant but poor correlation of bile and liver DMBA levels with EROD activities for both PCB congeners (Foster et al. 1996). The 2HxCB dietary exposures were run side-by-side with experiments that reported a strong correlation of aryl hydrocarbon hydroxylase activity with hepatic 2HxCB concentration and increased EROD with 2HxCB exposure (da Costa and Curtis 1995). However, the bile and liver [^{3}H]DMBA levels from our experiments were not strongly associated with the reported EROD activities (data not shown). There was no direct measurement of CYP1A induction in 3HxCB-fed fish but 10 weeks after i.p. 3HxCB exposure EROD activities

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Table 3. Mean biliary and hepatic tissue [^{3}H]DMBA equivalents 16 h after i.p. injection with 10 nmol [^{3}H]DMBA·g fish^{-1} that were i.p. injected with 50 or 250 µg 2HxCB·g fish^{-1} or 5 or 25 µg 3HxCB·g fish^{-1} 4 weeks earlier.

	PCB	Bile		Liver			
n	µg/g	nmol·g^{-1}	% dose·g^{-1}	nmol·g^{-1}	% dose·g^{-1}	nmol[a]	% dose[a]
2HxCB							
6	0	135.6[a]	28.2	7.2	1.4	2.3	0.48
		(32.1)	(7.5)	(0.9)	(0.2)	(0.3)	(0.07)
5	50	57.8[b]	11.0	5.6	1.1	2.0	0.38
		(5.0)	(0.8)	(0.9)	(0.2)	(0.3)	(0.06)
6	250	95.2[a,b]	18.4	5.5	1.0	2.2	0.40
		(15.0)	(4.0)	(1.0)	(0.1)	(0.4)	(0.04)
3HxCB							
6	0	135.6[a]	28.2	7.2	1.4	2.3	0.48
		(32.1)	(7.5)	(0.9)	(0.2)	(0.3)	(0.07)
6	5	100.6[a,b]	19.0	5.1	0.9	2.2	0.37
		(20.1)	(4.3)	(1.1)	(0.1)	(0.3)	(0.05)
4	25	44.6[b]	9.1	4.1	0.9	1.8	0.35
		(3.8)	(0.8)	(1.0)	(0.2)	(0.5)	(0.13)

Note: One-way ANOVA using one-tailed p-value <0.05 and LSD multiple comparison. % dose data were analyzed by ANOVA using the arcsine of the square root.

[a]This is the total nmole and % dose, respectively, in the whole organ.

were induced at low doses and inhibited at high doses (Donohoe et al. 1995). Stimulated biliary excretion of [^{3}H]DMBA equivalents was expected with increased CYP1A hepatic content if metabolism was rate limiting for [^{3}H]DMBA elimination. However, 2HxCB and 3HxCB pretreatments that induced hepatic CYP1A were not directly associated with stimulated [^{3}H]DMBA biliary excretion. Inhibition of CYP1A-mediated oxidative metabolism by high hepatic 3HxCB concentrations perhaps explained reduced biliary excretion of [^{3}H]DMBA after i.p. doses (Table 4) and long-duration dietary exposures (Figs. 2 and 3) but does not explain the lack of association between CYP1A activity and [^{3}H]DMBA concentrations in bile and liver for 2HxCB exposed fish.

The absence of a direct association between biliary excretion of [^{3}H]DMBA and PCB pretreatments that induced the CYP1A system in other work was perhaps explained by modulation of other rate-limiting processes. Previous work in this laboratory demonstrated altered disposition and increased biliary excretion of a subsequent dose of dieldrin following pretreatment with dieldrin in rainbow trout (Shubat and Curtis 1986; Gilroy et al. 1994). Because dieldrin pretreatments failed to induce CYP1A, induction of a hepatic cytosolic binding protein was suggested as the mechanism of altered disposition (Gilroy et al. 1996). Another study suggested that biliary excretion rather than oxidative metabolism was rate limiting for temperature-modulated benzo[*a*]pyrene elimination in rainbow trout (Curtis et al. 1990). This was also suggested for other organic compounds such as pentachlorophenol, hexachlorobenzene, and mirex in rainbow trout (Niimi and Palazzo 1985).

Earlier reports of increased CYP1A in fish after 2HxCB exposure (Forlin and Lidman 1979) were attributed to TCDD contamination of the 2HxCB (James and Little 1978). Mass spectrometry revealed no evidence of trace contamination of the 2HxCB stock used in this study with TCDD or other high affinty AhR agonists (da Costa and Curtis 1995). The highest possible TCDD dose, calculated from the 2HxCB purity analysis detection limits for TCDD, was less than 4 pg TCDD·g fish^{-1}. This dose was less than half the TCDD dose that failed to induce CYP1A or EROD in carp (van der Weiden et al. 1994). In addition, long-term feeding of 2HxCB to rainbow trout increased EROD and AHH activities, which were positively correlated with 2HxCB liver concentration (da Costa and Curtis 1995), indicating that 2HxCB absorption and target organ dose were contributing to activity variability.

Target organ dose can be useful in explaining biological responses, and although this study did not measure liver or body burden of 2HxCB or 3HxCB, the exposure dose should be sufficient for understanding the relationship between PCB exposure and altered DMBA disposition. The accumulation rates for 2HxCB and 3HxCB should be similar because the partition coefficients for the two compounds are similar with 2HxCB and 3HxCB having logK_{ow} of 6.92 and 7.42, respectively (Hawker and Connell 1988). Bioaccumulation rates in zebrafish were similar with 2HxCB and 3HxCB having log bioconcentration factors of 5.65 and 5.97, respectively (Fox et al. 1994), and accumulation of PCBs in blue mussels (*Mytilus edulis*) were strongly correlated with logK_{ow} for both coplanar and noncoplanar PCB congeners (Bergen et al. 1996). Field studies have shown that some noncoplanar PCBs can bioaccumulate to higher concentrations than coplanar PCBs, which may be due to the source material having initially higher levels of noncoplanar congeners (Kannan et al. 1998). However, laboratory studies with mice (De Jongh et al. 1993) show that liver accumulation is greater for 3HxCB than for 2HxCB. This could be explained by CYP1A2 acting as a binding protein for coplanar PCBs in mammals (Diliberto et al. 1997). CYP1A2 is not thought to be present in fish (Nelson et al. 1996) but its existence in fish is controversial (Berndston and Chen 1994). Differences between

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Fig. 2. Mean biliary and liver [^{3}H]DMBA equivalents as % dose·g tissue^{-1} 16 h after i.p. injection with 10 nmol [^{3}H]DMBA·g fish^{-1} that were fed 0 (open bars), 60 (hatched bars), or 220 (solid bars) ng 2HxCB·g fish^{-1}·day^{-1} for 4, 8, or 12 weeks. Error bars are standard error. *Significantly different from controls at a one-tailed p-value < 0.05. Controls were a grand mean of 8- and 12-week controls as 4-week controls were not available. Note difference between Y-axis scales.

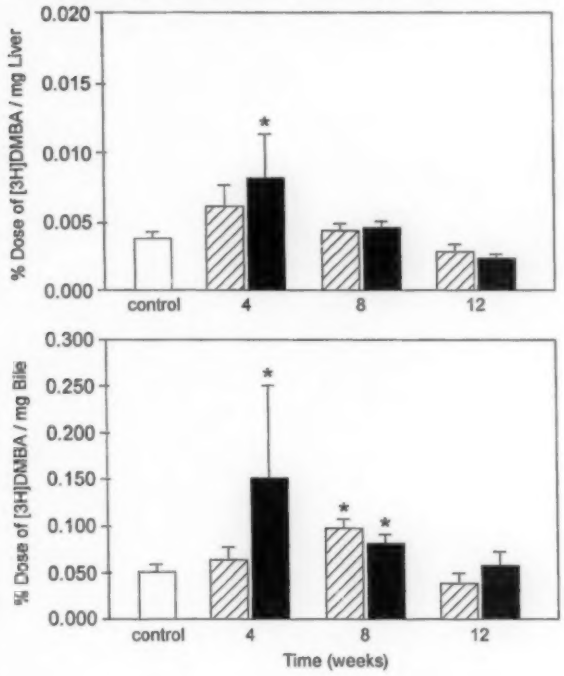
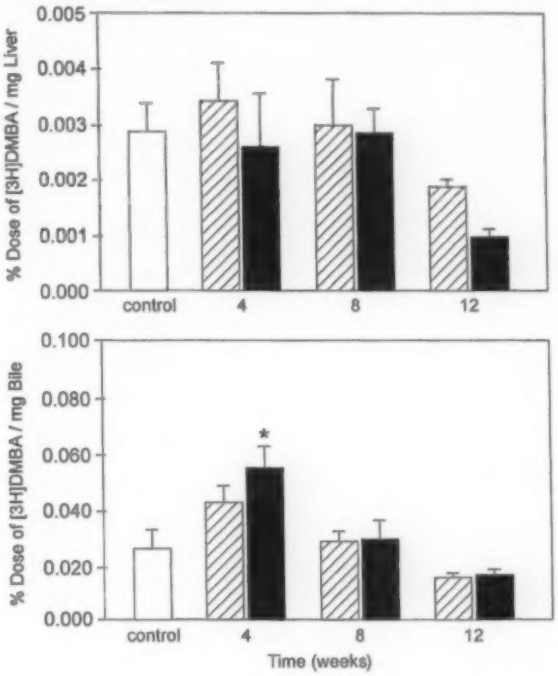


Fig. 3. Mean biliary and liver [^{3}H]DMBA equivalents as % dose·g tissue^{-1} 16 h after i.p. injection with 10 nmol [^{3}H]DMBA·g fish^{-1} that were fed 0 (open bars), 2 (hatched bars), or 8 (solid bars) ng 3HxCB·g fish^{-1}·day^{-1} for 4, 8, or 12 weeks. Error bars are standard error. *Significantly different from controls at a one-tailed p-value < 0.05. Controls were a grand mean of 4-, 8-, and and 12-week controls. Note difference between Y-axis scales.



whole-body and liver accumulation rates for coplanar and noncoplanar PCBs cannot be ruled out as most studies measured only one or the other. However, experiments that were run side-by-side with this work and reported by da Costa and Curtis (1995) showed a linear accumulation of 2HxCB in muscle and liver through 12 weeks of feeding.

In addition to parent compound effects, PCB metabolites may be important in PCB–PAH interactions. Methylsulfone metabolites of tetra-, penta-, and hexa-chlorobiphenyls increased cytochrome P450 levels and the activities of 7-ethoxycoumarin and AHH in rats (Kato et al. 1995). Hydroxy metabolites of PCBs can bind with thyroid hormone receptors (McKinney et al. 1987), affecting thyroid hormone levels, which can be an important modulator of overall metabolic activity. Weeks elasped between i.p. pretreatments and [^{3}H]DMBA challenge doses, or fish were fed lower doses for 4–12 weeks prior to the PAH injection. If metabolism was a factor in any of the observed results, a significant amount of time was allowed for biotransformation of the highly persistent PCBs used. The amount of biphenyl chlorination can affect PCB metabolite formation, with PCB metabolite production increasing as the amount of biphenyl chlorination decreased. Therefore, less chlorinated PCBs may have a greater effect on altering disposition than the more highly chlorinated PCBs such as 2HxCB or 3HxCB.

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Accumulation and recycling of PCBs and PAHs in artificially eutrophied Lake 227

Jeff D. Jeremiason, Steven J. Eisenreich, and Michael J. Paterson

Abstract: The influence of lake trophic status on the cycling and burial of polychlorinated biphenyls (PCB's) and polycyclic aromatic hydrocarbons (PAH's) was examined in Lake 227 (L227), an artificially eutrophied lake in the Experimental Lakes Area, northwestern Ontario, Canada. Sedimentary accumulation of PCB's, PAH's, and organic carbon (OC) was determined pre- and post-eutrophication in L227 and compared with accumulation in other regional lakes. Mass and OC accumulation increased an average of 1.4 and 2.0 times, respectively, since nutrient addition began in June 1969. ΣPCB and ΣPAH sediment accumulation rates and profiles in L227 were similar to those in Lake Superior and other proximate and midlatitude lakes unimpacted by point sources. Eutrophication did not increase contaminant accumulation. In general, individual PAH accumulation rates declined following eutrophication, which coincided with similar signals elsewhere. Perylene declined markedly (4 times) since eutrophication as a result of decreased in situ formation. An increase in OC accumulation did not enhance contaminant accumulation in L227 because phytoplankton community structure shifted to species characterized by lower bioaccumulation factors, and water column recycling rates were high. Accumulation rates of mass, OC, PCB's, and PAH's, when compared with ice-free settling fluxes in 1993 and 1994, exhibited similar recycling ratios in eutrophic L227 and oligotrophic L110 due to the efficient preservation of organic matter in sediments.

Résumé : L'influence de l'état trophique d'un lac sur le cycle et l'enfouissement des polychlorobiphényles (PCB) et des hydrocarbures aromatiques polycycliques (HAP) a été étudiée dans le lac 227 (L227), un lac artificiellement eutrophisé de la région des lacs expérimentaux, dans le nord-ouest de l'Ontario, au Canada. L'accumulation dans les sédiments des PCB, des HAP et du carbone organique (CO) a été mesurée avant et après l'eutrophisation du L227 et comparée à l'accumulation dans d'autres lacs de la région. Les accumulations de matière et de CO se sont accrues en moyenne par un facteur 1,4 et par un facteur 2,0, respectivement, depuis que l'apport de nutriants a débuté, en juin 1969. Les taux d'accumulation dans les sédiments et les profils de ΣPCB et ΣHAP dans L227 étaient semblables à ceux du lac Supérieur et d'autres lacs voisins situés à une latitude moyenne qui n'ont pas été affectés par des sources ponctuelles. L'eutrophisation n'a pas accru l'accumulation de contaminants. En général, les taux d'accumulation des divers HAP ont diminué après l'eutrophisation, ce qui a coïncidé avec des observations similaires faites ailleurs. La concentration de pérylène a chuté de façon marquée (4 fois) depuis l'eutrophisation par suite d'une réduction de sa formation in situ. L'accroissement de l'accumulation de CO n'a pas entraîné un accroissement de l'accumulation de contaminants dans L227 parce que la structure de la communauté phytoplanctonique s'est modifiée pour inclure des espèces caractérisées par de faibles facteurs de bioaccumulation et que les taux de recyclage dans la colonne d'eau étaient élevés. Les taux d'accumulation de matière, de CO, de PCB et de HAP, quand ils étaient comparés aux flux de sédimentation en eau libre de glace de 1993 et 1994, ont montré des ratios de recyclage similaires dans le lac eutrophe L227 et le lac oligotrophe L110 en raison de la préservation importante de matière organique dans les sédiments.

[Traduit par la Rédaction]

Introduction

The production, cycling, and burial of organic matter (OM) play a major role in hydrophobic organic chemical (HOC) cycling, transport, and burial in aquatic systems (Eisenreich 1987; Eisenreich et al. 1989; Baker et al. 1991; Sanders et al. 1996; Lipiatou et al. 1997). Polychlorinated biphenyls (PCB's) and polycyclic aromatic hydrocarbons (PAH's) have a strong affinity for natural OM (Schwarzenbach et al. 1993). Increases in particulate and dissolved OM derived from increased primary production should enhance retention of HOC's added from the atmosphere and the surrounding watershed, leading to increased sedimentary accumulation rates and inventories. Whole-lake equilibrium or fugacity models (Mackay and Paterson 1991) predict enhanced HOC burial in aquatic systems with increased biomass. HOC burial increases with higher OM settling fluxes and accumulation rates and is reflected in increased fugacity capacities (Z values) of the particulate phase (e.g., Mackay and Paterson 1991). Cycling of HOC's within the water column may also be impacted by eutrophication. For example,

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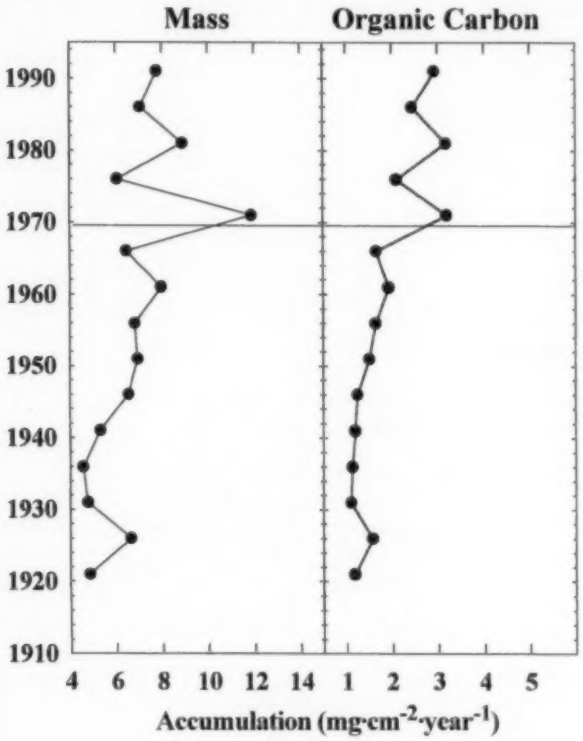
Fig. 1. Focus-corrected accumulation rates of mass and OC in L227.



recycling of OM in the epilimnion, at the top of the hypolimnion, and near the sediment–water interface is modified by changes in oxygen and nutrient levels caused by eutrophication (Gunnarsson et al. 1995). Artificially eutrophied Lake 227 (L227) offers the unique opportunity to investigate effects of increased primary production on HOC accumulation rates and cycling.

L227 is a small lake (surface area = 5.0 ha, volume = 2.21×10^5 m^3) with a maximum depth of 10 m and a drainage area of 34.4 ha and is located in the Experimental Lakes Area (ELA) of northwestern Ontario, Canada (93°41′W, 49°41′N). L227 was involved in experiments initiated in 1969 to determine whether C, N, and (or) P limited phytoplankton growth (Schindler 1974). Phosphorus was added to the epilimnion during the stratified period at a rate of 0.48 g·m^{-2}·year^{-1}, and N was added at an N to P mass ratio of 13:1 from 1969 to 1974 and 5:1 from 1975 to 1990; N addition ceased after 1990 (Schindler 1974; Findlay et al. 1994). Artificial P loading rates are about 10 times natural P loading by wet deposition and runoff (Findlay et al. 1994). Nutrient additions resulted in immediate increases in phytoplankton biomass and changed the phytoplankton community structure from one dominated by primarily chrysophytes to one dominated by cyanobacteria (Findlay et al. 1994). Increases in phytoplankton biomass increased P, N, and C accumulation (Findlay et al. 1994; Wolfe et al. 1994). This work examines PCB and PAH accumulation and recycling and relates these to changes in C recycling and accumulation.

The objectives of this study were to (*i*) determine the effects of eutrophication on PCB and PAH accumulation rates, profiles, and inventories in L227 and (*ii*) assess the cycling of PCB's and PAH's in eutrophic L227 relative to other ELA lakes. The first objective was addressed by comparing L227 with other midlatitude and ELA lakes (L110 and L375) presumably unimpacted by point sources and obtaining contaminants from atmospheric deposition. The second objective was achieved by comparing settling flux to accumulation (recycling) ratios and HOC concentrations on suspended particles, settling particles, and bottom sediments in L227 with those in L110 and other systems. L110 is oligotrophic, located about 10 km from L227, and has similar lake and watershed areas and water volumes.

Methods

Sediment coring and dating

Sediment cores were collected from L227 and L110 in February 1994 and September 1993, respectively, from the deepest part of each lake using a freeze-corer (Crusius and Anderson 1995). The brass freeze-corer was 6 × 31 × 61 cm and tapered to a wedge at the closed bottom. Sediment was collected by adding a slurry of dry ice and methanol to the corer and freezing the sediment to its outside. The corer was insulated on three sides with closed-cell ensolite padding covered with fiberglass.

The L227 core was sectioned while frozen in 5-year intervals according to visible sediment varves. About 0.5 cm of sediment was removed (by planing) from the sides of the core to remove smeared material. The light-colored laminae are deposited during summer to early winter and consist mainly of remains from summer planktonic production (Wolfe et al. 1994). The dark, thinner laminae likely deposit in late winter and consist mainly of benthic algae (Wolfe et al. 1994). Certain phytoplankton taxa specific to a given year were used as biomarkers and aided in the dating of some sections deposited after eutrophication (Wolfe et al. 1994). The mass sedimentation rate was determined for each section based on the surface area and dry weight of the section and the number of years represented by each section. The sediment core from L110 was 46 cm in length and sectioned into 1-cm increments. The sedimentation rate of 8.0 mg·cm^{-2}·year^{-1} in L110 was estimated based on the linear regression of excess ^{210}Pb versus accumulated mass in the upper 8 cm of the sediment core (Jeremiason 1997).

Sediment focusing factors (FF's) were used to correct accumulation rates for the movement of sediments from shallower, nondepositional areas to deeper depositional zones (Wong et al. 1995; Simcik et al. 1996). The FF may be estimated as the ratio of the unsupported ^{210}Pb inventory in the core to the ^{210}Pb inventory expected based on atmospheric deposition (Eisenreich et al. 1989; Urban et al. 1990). Recent ^{210}Pb dating is complicated in L227 due to addition of ^{226}Ra to the epilimnion in 1970 (Crusius and Anderson 1995). As a result, P was used to calculate an FF in L227. A yearly P budget for the L227 basin was constructed previously (Findlay et al. 1994). Artificial and natural P inputs less outflow totaled 565 kg or 1.13 mg·cm^{-2} from 1969 to 1994. Phosphorus inventory in the sediment core post-eutrophication was 1.67 mg·cm^{-2}, leading to an FF of 1.5. Phosphorus accumulation also increased prior to the addition of P to L227 (Fig. 1) due to natural eutrophication or diffusion of P from post- to pre-eutrophied sediment. Since the sediments are laminated, there is little bioturbation, and consequently, the gradual P increase since about 1940 was assumed to result from diffusion. Accounting for diffusion, the P inventory post-eutrophication was 1.89 mg·cm^{-2}, leading to an FF of 1.7. These two estimates bracket a previously determined FF of 1.6 by

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Crusius and Anderson (1995) determined with the ^{210}Pb technique and was selected as the FF.

Sediment traps

The sediment traps and their deployment schedules are discussed in detail elsewhere (Jeremiason 1997; Jeremiason et al. 1999). Briefly, large 1-m-diameter sediment traps were deployed in the hypolimnia (depth = 6 m) of L227 and L110 and sediment was collected every 2 weeks during the ice-free seasons of 1993 and 1994. The larger traps were used to collect sufficient material for precise PCB and PAH quantification. Smaller traps with a 10:1 height to diameter aspect ratio were deployed concurrently to quantitatively assess mass and C fluxes (Elser et al. 1995).

Laboratory procedures

Analysis of PCB's and PAH's in the sediment cores is described in detail elsewhere (Jeremiason 1997). Briefly, a known amount of freeze-dried sediment (1–2 g) was placed in a 30-mL Pyrex extraction thimble and extracted with dichloromethane in a Soxhlet apparatus for 24–36 h. The PCB surrogates, added prior to extraction, consisted of 3,5-dichlorobiphenyl (IUPAC congener No. 14), 2,3,5,6-tetrachlorbiphenyl (IUPAC No. 65), and 2,3,4,4′,5,6-hexachlorobiphenyl (IUPAC No. 166). The PAH surrogates consisted of deuterated PAH's (Cambridge Isotopes): d10-fluorene, d10-fluoranthene, and d12-perylene. The extracts were split by volume for PCB (75%) and PAH (25%) analyses. PCB extracts were fractionated by liquid–solid chromatography using 8 g of 1.25% water-deactivated Florisil (Jeremiason et al. 1994). PAH extracts were fractionated similarly on a column containing 7 g of 5% water-deactivated silicic acid. PCB congeners were separated by gas chromatography using a 60 m × 0.25 mm inside diameter dimethyldiphenylpolysiloxane capillary column with a 0.25-μm film thickness (DB-5, J&W Scientific). PCB's were analyzed on a Hewlett-Packard 5890 gas chromatograph equipped with a ^{63}Ni electron capture detector and an Hewlett-Packard 7673 autosampler. All PCB concentrations were corrected for the recovery of PCB surrogate No.166, which averaged 95 ± 10%. PCB No. 166 was chosen as the congener to correct for surrogate recovery based on seven samples consisting of only solvent spiked with the PCB calibration standard containing no internal standards. Surrogate recoveries of Nos. 14, 65, and 166 were not statistically different in these seven samples (Jeremiason 1997). PAH's were separated on a 30 m × 0.25 mm inside diameter capillary column with a 0.25-μm film thickness (DB-5MS, J&W Scientific). The mass spectrometric detector (Hewlett-Packard 5971 MSD) was operated in selective ion monitoring mode. PAH concentrations were corrected to the nearest eluting surrogate. PAH surrogate recoveries were 83 ± 13, 87 ± 12, and 73 ± 9%, respectively, for d10-fluorene, d12-fluoranthene, and d12-perylene. Subsamples of each core section were removed and analyzed for organic carbon (OC) according to Stainton et al. (1977).

Results and discussion

Mass and carbon accumulation

Sediment focus-corrected mass accumulation rates in L227 increased an average of 1.4 times since eutrophication from 5.9 ± 1.1 (±1 SD) to 8.3 ± 2.3 $mg \cdot cm^{-2} \cdot year^{-1}$ (Fig. 1). Mass accumulation rates were similar to values determined previously for cores in L227 (Wolfe et al. 1994; Crusius and Anderson 1995). OC accumulation in L227 increased an average of 2 times after nutrient addition (Fig. 1). OC content increased 1.5 times from an average of 232 to 339 mg $OC \cdot g^{-1}$ following eutrophication resulting in greater OC accumulation relative to mass. Assuming that the mass flux increase after eutrophication was due entirely to OM containing 400 mg $OC \cdot g^{-1}$ (typical of L227 sediment trap material; Jeremiason 1997), an OC content of 270 $mg \cdot g^{-1}$ (actual = 339 $mg \cdot g^{-1}$) was predicted. Thus, increased OC content does not fully explain higher OM accumulation. Shifts in phytoplankton community structure from one dominated by chrysophytes to one dominated by the OC-rich cyanophytes post-eutrophication (Findlay et al. 1994) may have increased OC content. Decreased OC recycling caused by anoxia in the hypolimnion could also increase OC content post-eutrophication (Gunnarsson et al. 1995).

PCB and PAH accumulation

Increased OM accumulation in L227 post-eutrophication may lead to increased sequestering of PCB's and PAH's and subsequent increased burial rates. For example, with a constant K_{oc} (OC-normalized partition coefficient, litres per kilogram), air–water fugacity and equilibrium models predict a twofold increase in HOC accumulation due to the higher C accumulation (Mackay and Paterson 1991; Schwarzenbach et al. 1993). Differences in K_{oc} values between phytoplankton pre- and post-eutrophication may modify HOC sequestering relative to OC. L227 is currently dominated by blue-green phytoplankton, whereas chrysophytes and diatoms dominated pre-eutrophication (Findlay et al. 1994). Stange and Swackhamer (1994) reported bioconcentration factors for PCB's with octanol–water partition coefficients (K_{ow}) less than 10^6 to be 5–10 times lower for the blue-green *Anabaena* species relative to the diatom *Synedra*. Thus, changes in phytoplankton community structure may decrease contaminant accumulation rates despite increased OC accumulation.

Temporal accumulation rates pre- and post-eutrophication derive from temporal changes in PCB and PAH loadings. Sediment PCB and PAH accumulation profiles frequently reflect production and use (e.g., Eisenreich et al. 1989; Wong et al. 1995; Muir et al. 1996; Simcik et al. 1996). In the case of PCB's, production peaked in the middle to late 1960's and was restricted in the early 1970's in the United States and Canada, both events contemporaneous to artificial nutrient additions in L227. PAH accumulation patterns similar to those in Lake Superior (Gschwend and Hites 1981) may be expected based on locale and since ELA is not proximate to PAH sources. PAH's in ELA sediments should reflect a regional background atmospheric PAH source, possibly impacted by local fire events.

PCB accumulation

To determine the effects of eutrophication on PCB accumulation rates and profiles, the L227 core is compared with one in Lake Superior (Fig. 2). ΣPCB accumulation rates in the sediments of L227 maximize at the onset of nutrient addition in 1969 at 0.22 $ng \cdot cm^{-2} \cdot year^{-1}$ and decrease to 0.12 $ng \cdot cm^{-2} \cdot year^{-1}$ at the surface (Fig. 2). PCB accumulation reaches a maximum immediately following nutrient addition due to increased mass accumulation (Fig. 1) coupled with maximum atmospheric ΣPCB concentrations achieved between 1966 and 1976. Increased mass accumulation may reflect uneven sedimentation in L227 or uncertainty in core dating. There was a large mass of sediment containing no varves in the core slice immediately following eutrophication. The midpoint of this section was determined to have been deposited in middle to late 1971 based on a char-

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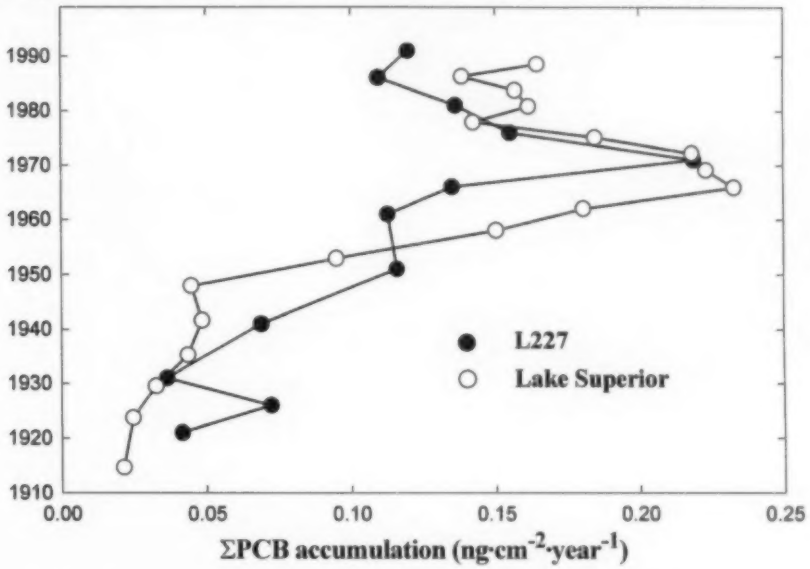
Fig. 2. L227 and Lake Superior site SJEII and NOAA site 3 (Jeremiason 1993) ΣPCB accumulation profiles.



acteristic *Synedra* species that first appeared in L227 in June 1971 (Wolfe et al. 1994). The L227 ΣPCB accumulation profile is consistent with Great Lakes cores and similar to a core from the Duluth basin of Lake Superior (Fig. 2), the Great Lake closest in proximity to ELA and least impacted by point sources (Eisenreich 1987). ΣPCB accumulation rates in L227 decreased by a factor of 2 from 0.22 ng·cm^{-2}·year^{-1} in 1971 (midpoint date) to 0.12 ng·cm^{-2}·year^{-1} at the surface despite a doubling in OC accumulation post-eutrophication. In a similar fashion, Lake Superior ΣPCB accumulation decreased after 1970 to 1990 by 1.5–3 times (Jeremiason 1993). Mass sedimentation rates in Lake Superior are similar to those in ELA lakes, while terrestrial inputs and bank erosion in the former contribute much of the mass and OC content (about 20–50 mg C·g^{-1}; Johnson et al. 1982). Also, Lake Superior sediments are not varved with mixed depths of about 0.5–1 cm (Eisenreich 1987). Similarities between ΣPCB accumulation rates and profiles from L227 and Lake Superior suggest that eutrophication had little effect on PCB accumulation.

In L110, the surficial ΣPCB sediment accumulation rate was 0.24 ng·cm^{-2}·year^{-1} as compared with 0.19 ng·cm^{-2}·year^{-1} in L227 (not corrected for focusing). An FF could not be determined due to a homogeneous ^{210}Pb activity from 8 to 46 cm. An FF of 2 was estimated by dividing the surface area at the thermocline by the lake surface area (Elser et al. 1995). Thus the sediment focusing-corrected ΣPCB accumulation rate was 0.12 ng·cm^{-2}·year^{-1} in both lakes. Surficial ΣPCB concentrations were also greater in L110 by a factor of 2.5 (104 versus 41 ng PCB·g OC^{-1}). Thus, a two-fold increase in OC sequestration in L227, which could lead to an increase in PCB and PAH sequestration relative to L110, was offset by lower chemical concentrations. In nearby L375, focus-corrected ΣPCB accumulation since 1980 was also 0.12 ng·cm^{-2}·year^{-1} (Muir et al. 1996). Similar accumulation rates of 0.06–0.43 ng·cm^{-2}·year^{-1} have been reported for midlatitude lakes (Muir et al. 1996). An increase in ΣPCB accumulation due to eutrophication was not observed in L227. A dramatic change in phytoplankton community structure from a chrysophyte- to a cyanobacteria-domnated community characterized by lower bioconcentration factors is the likely reason that PCB accumulation was not enhanced.

PCB homolog distributions in the sediment prior to nutrient addition were dominated by 3-, 4-, and 5-chlorinated congeners, while post-eutrophication sediments exhibited a more uniform homolog distribution (Fig. 3). Prior to eutrophication, homolog distributions were similar to L110 sediments and present-day settling particles from both lakes. This is evidence that changes in phytoplankton species can significantly alter PCB distributions. The accumulation of hexachlorinated PCB's, specifically Nos. 153 and 138, did not decrease after about 1970 as was observed for the 3-, 4-, and 5-chlorinated PCB's (Fig. 4). The change in phytoplankton community structure exerted a greater effect than increased particle concentrations. More efficient PCB removal due to higher OC fluxes post-eutrophication would impact all PCB's, not just the hexachlorinated congeners. Stange and Swackhamer (1994) reported bioaccumulation factors for the cyanophyte *Anabaena* to be up to 10 times greater than bioaccumulation factors for the diatom *Synedra* for PCB congeners with log K_{ow} of about 7 and above. Congener Nos. 153 and 138 have log K_{ow}'s of 6.92 and 6.83, respectively. An effect was not observed for hepta- and higher chlorinated PCB's, since they are present at low concentrations.

PCB recycling

The effects of eutrophication on in-lake recycling of PCB's in L227 were assessed by comparing L227 with L110. ΣPCB settling fluxes in L227 (Jeremiason 1997; Jeremiason et al. 1999) measured in sediment traps during the stratified period in 1993 (June 1 to September 9) and 1994 (May 18 to September 7) were on average 7–10 times greater (10.0 ±

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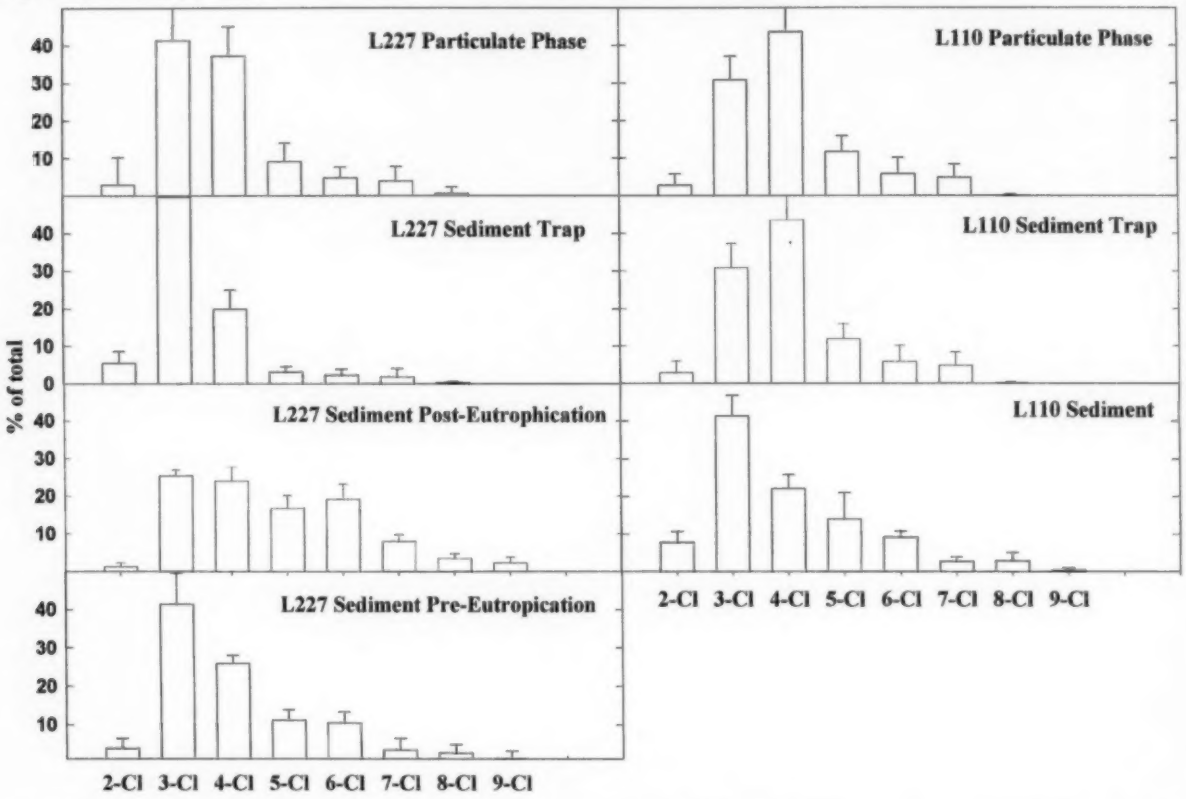
Fig. 3. PCB homolog profiles in water column and settling particles and bottom sediments in L227 and L110.



2.5 in 1993 and 6.9 ± 2.0 in 1994) than surficial accumulation rates in bottom sediments (Fig. 5). Settling fluxes were also corrected for focusing within the water column by dividing by the surface area at the thermocline by the surface area of the lake (Elser et al. 1995). The ratios of the settling particle flux to bottom sediment accumulation rates (recycling ratio, RR) for ΣPCB of 7–10 were greater than the RR's for OC and mass of 3–4. PCB's are associated with the more labile OC fraction that is preferentially mineralized, releasing PCB's into solution (Baker et al. 1991). In oligotrophic L110, RR's for PCB's, OC, and mass were similar at 3–4 (Fig. 5).

The RR's for PCB homologs (Fig. 5) generally decreased with increasing chlorination in L227. However, no distinct pattern was observed in L110 where ΣPCB RR's were lower. Baker et al. (1991) reported PCB RR's ranging from 10 to 500 in Lake Superior, with the more soluble congeners exhibiting higher ratios than PCB's of lower solubility. They hypothesized that benthic recycling of OM preferentially released the more soluble congeners, but the more hydrophobic congeners were more efficiently incorporated into bottom sediments. Benthic recycling within the depositional areas of L227 is unlikely, since there is no benthic community as reflected by varved sediments. Sanders et al. (1996) reported for Esthwaite Waters, U.K., PCB RR's from 8 to 23 with only a slight dependence on solubility. ΣPCB RR's in Lake Michigan range from about 3 to 6 and in Lake Ontario from about 1 to 2 based on settling particle fluxes and bottom sediment accumulation rates (Lefkovitz 1987; Oliver et al. 1989; Golden 1994; Wong et al. 1995).

Settling, suspended, and surficial sediments in L110 have nearly identical ΣPCB concentrations (Fig. 6) and homolog distributions (Fig. 3). However, settling particles have 1.5–4 times higher ΣPCB concentration than suspended or surficial sediments (Fig. 6) in L227. Settling particles are more enriched in less hydrophobic congeners as well (Fig. 3). Microscopic analysis showed that phytoplankton dominated both suspended (Findlay et al. 1994; Jeremiason 1997) and settling particles (Jeremiason 1997), but species composition was different, leading to differences in ΣPCB concentration. Suspended particles in L227 were composed mostly of cyanophytes throughout the stratified period. The highest ΣPCB concentrations were measured in May in L227 (Fig. 6). Settling particles during stratification were dominated by cyanophytes only during the two trap deployments following a *Microcystis* crash in August 1994 (Jeremiason 1997). In these two trap deployments, ΣPCB concentrations (28 and 33 ng·g OC^{-1}) were similar to those in suspended solids (33 ± 17 ng·g OC^{-1}) and surficial sediments (Fig. 6). Thus, cyanophytes likely comprise the bulk of surficial sediments (Wolfe et al. 1994), while the chrysophytes and diatoms that dominate May–July L227 trap material are efficiently recycled. We hypothesize that more efficient recycling of diatoms and chrysophytes in L227 relative to

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Fig. 4. PCB homolog accumulation rate profiles in the L227 sediment core.

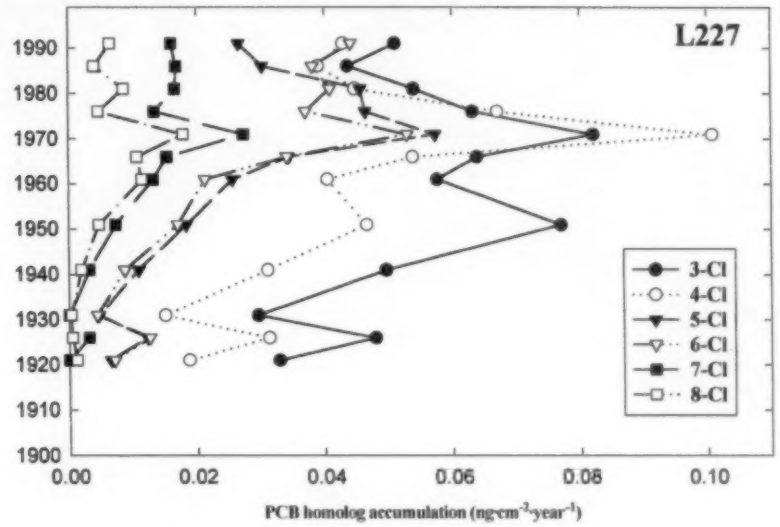
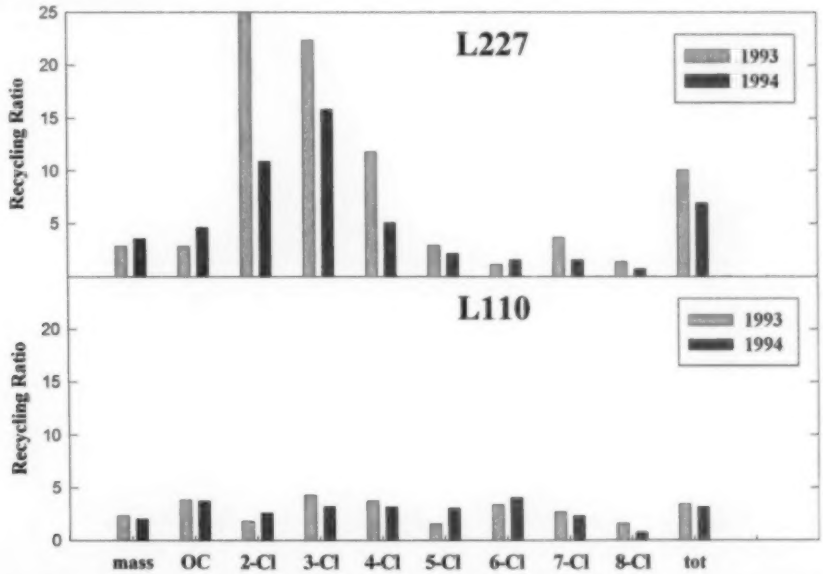


Fig. 5. Recycling ratios (settling particle flux during stratification divided by annual surficial sediment accumulation rate) of mass, OC, and PCB homologs in L227 and L110.



L110 results in ΣPCB RR's of 7–10 (Fig. 5). Prior to the *Microcystis* crash, settling solids in L227 had much higher ΣPCB concentrations (105 ± 33 ng·g OC^{-1}), values similar to chrysophyte-dominated L110. It is unclear why there is not as efficient recycling of PCB's in L110. However, the current L110 ΣPCB concentration (104 ng·g C^{-1}) in surficial sediment is greater than the maximum L227 ΣPCB concentration found in 1966 (82 ng·g C^{-1}). If recycling lowers PCB concentrations on solids prior to permanent burial (e.g., Baker et al. 1991), then PCB recycling was likely greater in L227 than in L110 even prior to eutrophication. Dissolved PCB concentrations were relatively constant from June to September 1994 in L227 and virtually identical in L110 (Jeremiason et al. 1999).

PAH accumulation and recycling

The sediment core from L227 was analyzed for a suite of 24 PAH's (Table 1). The ΣPAH (n = 24) accumulation profile in L227 dates back to 1919 and thus does not integrate all industrially derived PAH's (Fig. 7, top). Analogous to the PCB profiles, a peak in PAH accumulation immediately followed onset of eutrophication corresponding to high mass accumulation in the 1971 section. The accumulation of most PAH's decreased following eutrophication (Fig. 7). Whether

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Table 1. L227 sediment core focus-corrected inventories, 1919–1994.

Compound	Abbreviation	Inventory ($ng \cdot cm^{-2}$)	Surface accumulation ($ng \cdot cm^{-2} \cdot year^{-1}$)	Lake Superior surficial accumulation[a]
Fluorene	Flr	9.0	0.05	0.02
1-Methylfluorene	1mFlr	19.6	0.11	0.05
Phenanthrene	Phen	58.7	0.34	0.19
Anthracene	Ant	7.0	0.03	0.03
2-Methylphenanthrene	2mPhen	20.1	0.12	0.07
4,5-Methylenephenanthrene	4,5mPhen	22.8	0.07	0.02
1-Methylphenanthrene	1mPhen	21.9	0.11	na
3,6-Dimethylphenanthrene	3,6DmPhen	5.3	0.06	na
Fluoranthene	Flrt	61.9	0.26	0.32
Pyrene	Pyr	95.3	0.93	0.23
Retene	Ret	152.9	3.07	0.11
Benzo[*a*]fluorene	BaF	11.3	0.01	na
Benzo[*b*]fluorene	BbF	8.6	0.01	na
Benz[*a*]anthracene	BaA	11.1	0.00	0.10
Chrysene	Chry	24.4	0.05	0.25
Benzo[*b*+*k*]fluoranthene	Bb+kF	72.7	0.10	1.17
Benzo[*e*]pyrene	BeP	26.3	0.09	0.23
Benzo[*a*]pyrene	BaP	32.3	0.23	0.17
Perylene	Peryl	62.9	0.18	0.11
Indeno[1,2,3-*c*,*d*]pyrene	IP	58.3	0.07	0.47
Dibenzo[*a*,*c*+*a*,*h*]anthracene	DBA	5.9	0.00	0.07
Benzo[*g*,*h*,*i*]perylene	BghiP	52.4	0.07	0.30
Anthanthrene	Anthan	2.2	0.00	0.07
Coronene	Cor	33.3		0.00
Total PCB's	ΣPCB	7.8	0.12	0.09
Dichorinated PCB's	2-Cl	0.20	0.002	0.006
Trichlorinated PCB's	3-Cl	2.55	0.051	0.011
Tetrachlorinated PCB's	4-Cl	1.99	0.043	0.007
Pentachlorinated PCB's	5-Cl	1.14	0.027	0.014
Hexachlorinated PCB's	6-Cl	1.13	0.044	0.024
Heptachlorinated PCB's	7-Cl	0.48	0.016	0.019
Octachlorinated PCB's	8-Cl	0.28	0.006	0.004
Nonachlorinated PCB's	9-Cl	0.17	0.002	0.002

[a]NOAA site 3 sediment core (Jeremiason 1993).

Fig. 6. ΣPCB concentrations on suspended, settling, and surficial sediments in L227 and L110.

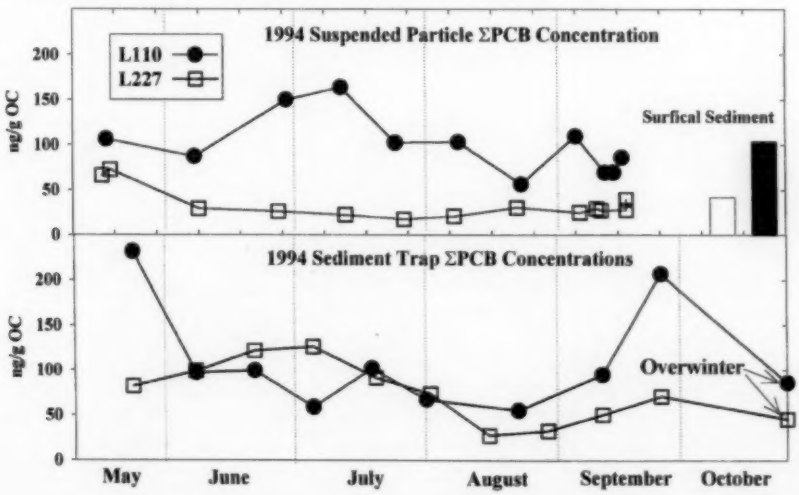

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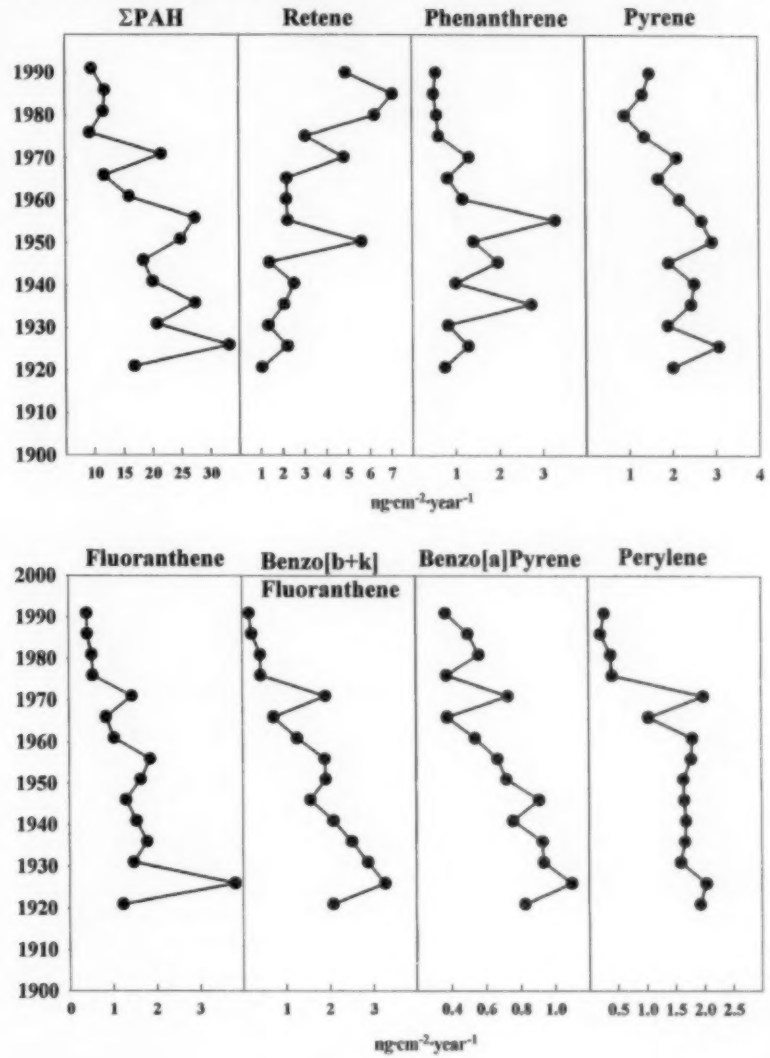
Fig. 7. PAH accumulation rates in the L227 sediment core.



this decrease was due to eutrophication or a general decrease in atmospheric deposition is unclear. Lockhart et al. (1993) reported a decrease of about 35% in ΣPAH (16 compounds) accumulation (9.3–6.3 ng·cm^{-2}·year^{-1}) from 1950 to the present at nearby L375. In L227, ΣPAH (24 compounds) accumulation has decreased from 25 to 9.6 ng·cm^{-2}·year^{-1} over the same period. Phenanthrene, fluoranthene, pyrene, and benzo[*a*]pyrene surface accumulation rates (Table 1) were similar to those reported for Lake Superior (Gschwend and Hites 1981). The only major PAH that increased following eutrophication was retene, which originates from pine resin and whose release is enhanced by burning (Sheffield et al. 1994). The L227 watershed was not burned, but a major forest fire occurred at ELA in 1980 and a lesser fire occurred in 1974. Retene is formed by microbial breakdown of abietic acid (Simoneit 1977). There is no evidence that eutrophication enhanced the accumulation of PAH's in L227.

Perylene exhibited the most marked PAH accumulation decline following eutrophication (4 times) (Fig. 7, bottom). Unlike other PAH profiles that generally increase with depth pre-eutrophication (Fig. 7), perylene accumulation was constant, as expected for an unchanging natural source. Lake Michigan sediments reflect anthropogenic coal use (Simcik et al. 1996), and benzo[*b*+*k*]fluoranthene predominates over perylene by a ratio of about 10:1, whereas in L227, this ratio was about 1:1. Perylene is generally found in greatest quantities in anoxic sediments rich in diatoms (e.g., Venkatesan 1988). Some have argued for in situ generation of perylene, while others have claimed a terrestrial source (e.g., Venkatesan 1988). L227 results suggest in situ formation impacted by eutrophication. A terrestrial source would have been unimpacted by eutrophication, unless a change in focusing occurred post-eutrophication. Perylene decreases may have resulted from decreases in diatom abundance coupled with

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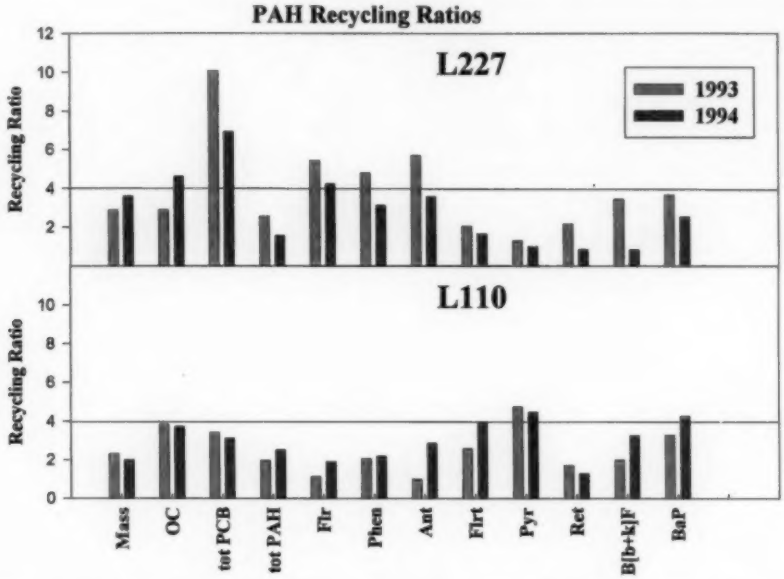
Fig. 8. PAH recycling ratios (settling particle flux during stratification divided by annual surficial sediment accumulation rate) in L227 and L110.



increased cyanobacteria following eutrophication. Boon et al. (1983) found no perylene in cyanobacterial mats rich in diatoms.

The RR's for ΣPAH (Fig. 8) were slightly lower than ΣPCB RR's, in both lakes, similar to other studies (Baker et al. 1991; Lipiatou et al. 1993, 1997; Sanders et al. 1996). Average ΣPAH RR's ranged from 2 to 3 in both L110 and L227. In L227, RR's were higher in 1993 than in 1994 and greatest for the lower molecular weight PAH's fluorene, phenanthrene, and anthracene. RR's for PCB's were also higher in 1993 than in 1994 in L227. Baker et al. (1991) reported the highest RR's for fluorene, phenanthrene, and benzo[*a*]pyrene (10–100) in Lake Superior, while the other PAH ratios were between 0.1 and 1.0. Similar results were reported for the Mediterranean Sea (Lipiatou et al. 1993, 1997). Sanders et al. (1996) reported PAH RR's in Esthwaite Water as about 1.0, except for phenanthrene, which was slightly higher at 2.5. In L110, ΣPAH RR's were similar to mass, OC, and PCB RR's, and there was little difference among individual PAH's (Fig. 8). PAH's not associated with primary soot particles are available to repartition among particle populations, while those associated with soot particles are largely refractory (Gustafsson and Gschwend 1998). There was no evidence indicating differences in cycling of PAH's between L227 and L110 caused by eutrophication.

HOC inventories

Inventories of PCB's and PAH's in L227 were compared with those in other systems to further assess the impact of eutrophication on HOC accumulation. The sediment inventory of PCB's and PAH's in L227 was determined by multiplying the concentration (nanograms per gram) by the dry mass accumulation (grams per square centimetre) in each section and summing over the entire core (Table 1). The ΣPCB inventory in L227 corrected for focusing (7.8 ng·cm^{-2}) was higher than inventories in Lake Superior, which ranged from 4.4 to 5.9 ng·cm^{-2} (Jeremiason 1993), similar to those in many midlatitude lakes (6.1–18.0 ng·cm^{-2}; Muir et al. 1996) but significantly lower than those in Lake Michigan (80–205 ng·cm^{-2}; Golden 1994) and Lake Ontario (600–1500 ng·cm^{-2}; Wong et al. 1995), which have been impacted by point and nonpoint sources. The PCB homolog distributions in L227 sediment are dominated by 3-, 4-, and 5-chlorinated PCB's, similar to those in midlatitude lakes (Muir et al. 1996) but somewhat different from those in Lake Superior, which have more 6- and 7-chlorinated congeners (Table 1). Lake Superior is more efficient in recycling the lower molecular weight PCB's, resulting in lower accumulation of these congeners. Lower molecular weight PAH's are also more prevalent in L227 than in Lake Superior, due to more efficient recycling in Lake Superior. However, the more hydrophobic PAH's are not as predominant in L227 as in Lake Superior (Table 1) or Lake Michigan (Simcik et al. 1996). This phenomenon is likely due to transport distance from sources.

Conclusions

Artificial nutrient addition to L227 beginning in 1969 doubled OC accumulation, but did not increase PCB or PAH accumulation rates. PCB accumulation rates and historic profiles are similar to those of regional lakes despite the striking transition to eutrophied status. The lack of increase in PCB and PAH accumulation and inventory is attributed to a shift in phytoplankton community structure from chrysophytes to cyanophytes characterized by lower bioconcentration factors, and efficient recycling of OM in L110 and L227, despite the latter having an anoxic hypolimnion for much of the year. PCB concentrations on phytoplankton were not diluted by greater phytoplankton biomass, since dissolved PCB concentrations were similar in L227 and

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oligotrophic L110 from June to September 1994. Rather, ΣPCB concentrations on suspended and settling solids were related to phytoplankton species composition. Lowest PCB concentrations were observed in L227 solids when cyanophyte species dominated. Higher PCB concentrations (similar to L110 PCB concentrations) were observed in L227 solids when chrysophytes and diatoms dominated. PCB recycling within the water column in artificially eutrophied L227 was greater than in oligotrophic L110, but was much lower than in Lake Superior. However, recycling efficiencies of mass, OC, and PAH's were similar between the two ELA lakes. This phenomenon also appears to be related to phytoplankton composition, with chrysophytes and diatoms being more efficiently recycled in L227 than cyanophytes.

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An alternative classification method for northern Wisconsin lakes

Edward E. Emmons, Martin J. Jennings, and Clayton Edwards

Abstract: Wisconsin has nearly 15 000 lakes with great variation in limnology, morphometry, and origin. Classification of lakes into groups is a continuing goal. This study examines two alternative approaches to lake classification, one common and the other somewhat novel. Both approaches used lake morphometry and limnological variables and were compared for ability to form groups and assign lakes to groups with a high probability of correct classification. The first approach used nonhierarchical cluster analysis to form lake groups and discriminant analysis to put lakes into these groups. The second approach formed lake groups by iterative dichotomous splitting of the sampling space into smaller and smaller subspaces. Each binary split was done using nonhierarchical cluster analyses on a subset of the original variables. This iterative splitting resulted in a hierarchical classification tree with reduced dimensionality in comparison with the original data set. At each branch, multiple logistic regression was used to place lakes into nodes of the tree. Validation of both approaches was performed with a resubstitution analysis of the model building data set as well as a separate validation data set. The decision tree method yielded significantly lower rates of misclassification and was more easily interpreted than the discriminant analysis approach.

Résumé : Le Wisconsin possède près de 15 000 lacs qui diffèrent fortement par leur limnologie, leur morphométrie et leur origine. La classification de ces lacs est un objectif à atteindre. Notre étude examine deux options pour cette classification, l'une courante et l'autre plutôt innovatrice. Les deux approches se fondent sur la morphométrie et les variables limnologiques des lacs, et nous avons comparé leur aptitude à former des groupes et à assigner les lacs à chaque groupe avec une forte probabilité de classification correcte. La première approche fait appel à une analyse typologique non hiérarchique pour constituer les groupes et une analyse discriminante pour placer les lacs dans ces groupes. La deuxième approche forme des groupes de lacs par division dichotomique itérative de l'espace d'échantillonnage en sous-espaces toujours plus petits. Chaque division binaire était faite à partir d'analyses typologiques non hiérarchiques portant sur un sous-ensemble des variables originales. Cette division itérative donnait un arbre de classification hiérarchique dont la dimensionnalité était réduite par rapport à la série originale. À chaque embranchement, une régression logistique multiple a servi à placer les lacs dans les noeuds de l'arbre. Nous avons effectué la validation des deux approches par une analyse de resubstitution de la série de données ayant servi à la modélisation, ainsi qu'avec une série séparée de données de validation. La méthode de l'arbre décisionnel a donné des taux de mauvaise classification nettement inférieurs et des résultats plus faciles à interpréter que l'analyse discriminante.

[Traduit par la Rédaction]

Introduction

Lentic systems are inherently variable in their physical, chemical, and biological properties. Hydrologic processes, soils in the watershed, landscape position, and basin morphometry all contribute to unique physical and chemical characteristics that effect biological processes. The uniqueness of individual lakes provides a challenge to formation of a widely applicable management framework. Effective management must allow for some generalization while taking into account characteristics of individual lakes that affect important ecological processes. Classification systems that account for ecologically meaningful variation provide a way to group lakes into units in which similar ecological processes operate and similar responses to anthropogenic impacts or management strategies can be expected. Classification systems that do this effectively can also provide a framework for research into ecological processes.

Ecological processes have been well studied in individual lentic systems, and the resulting information has formed the basis of several classification systems. The number and type of variables used to classify lakes depend on the objective. For example, variables that determine acid-neutralizing capability can be used to produce a classification of susceptibility to acidification (e.g., Pitblado et al. 1980). More complex data sets and statistical approaches might be desired to classify waters for suitability for fisheries manage-

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ment actions (e.g., Vehanen and Aspi 1996) or for susceptibility to cultural eutrophication or acidification (e.g., Willen et al. 1990). For a range of applications, the variables are similar, typically including the size of the drainage basin, area and depth of the lake, retention time, some estimate of lake productivity, various chemical parameters, or the suite of organisms of interest.

Although general agreement regarding appropriate variables can be found, statistical approaches vary considerably. In general, the data set used in any classification is large in size and complex. Such data sets are often statistically difficult to handle because they have high dimensionality, a mixture of data types such as continuous, ordinal, and nominal data, and nonhomogeneity of the data where different relationships exist between variables in different areas of the measurement space.

Criteria for classification can be computationally simplistic, consisting of a dichotomous key with a priori determination of the relative importance of individual variables (Bachmann et al. 1996), or alternatively, multivariate techniques can evaluate the variation in the data set, providing the basis for a posteriori assignment to groups.

Many different multivariate statistical methodologies have been applied to lake classification. Examples of various procedures include principal components analysis (PCA) and reciprocal averaging (Heywood et al. 1980), canonical correspondence analysis and detrended canonical correspondence analysis (Willen et al. 1990; Franklin et al. 1993), detrended correspondence analysis (Kauppinen and Vaisanen 1993), and some combination of a clustering algorithm and discriminant analysis (Tonn and Magnuson 1982; Vehanen and Aspi 1996; Momen and Zehr 1998). In each approach, data in many dimensions are summarized as linear combinations of variables and projected into a low-dimensional space.

These multivariate approaches often provide great insight into the relationships between variables and underlying group structure within the data. They also typically reduce dimensionality that allows many ecologically important variables to be considered. There are some weaknesses in these techniques: they are often difficult to interpret and to explain for management purposes, are often problematic in classifying observations not used to develop the classification (Verbyla 1986), and do not have great flexibility in the incorporation of hierarchical data structure and variable interactions into the classification (Loh and Shih 1997). Ecological data are often hierarchical in nature with interacting variables that affect both the diversity and abundance of the biota (Menge and Olson 1990; Angermeier and Winston 1998). A classification approach that explicitly incorporates these features may provide a powerful tool for classifying ecological units in a reliable and interpretable framework.

A family of techniques becoming increasingly popular for classification purposes that does this are tree-structured methods of which the best known is classification and regression tree analysis (CART) (Breiman et al. 1984). CART works by the recursive binary partitioning of the measurement space that maximizes the separation between predefined groups. Because of its recursive nature, the procedure results in a hierarchical tree where the response variable is split into smaller and smaller response groups using a subset of either continuous or categorical predictors at each branch in the tree. These tree-structured methods maintain variable interactions by using conditional information in handling nonhomogeneous relationships along the branches of the tree. This often results in a more easily understood and accurate classification function than is typically observed with discriminant function analysis (DFA), which also models group membership as a function of multiple predictor variables.

A problem with CART and DFA is that they require that group membership to be known in advance. Often the goal of classification analysis is to define a set of criteria that put observations into groups. In ecological terms, this is often thought of as clustering sites, species, or variables into groups by identifying an internal data structure using cluster analysis on a large multivariate data set (van Tongeren 1995). In typical cluster analysis, all variables are equally weighted and used to define groups in the whole of the measurement space. Because arbitrary group membership is seldom of interest, the group or class membership variable defined by cluster analysis is often used as the target for the other purpose of classification analysis, which is to uncover the predictive structure of the problem or to gain an understanding of what variables or interactions of variables determine when an observation is in one class versus another. In ecological uses of classification, this is usually done by examining the groups produced by cluster analysis with respect to some environmental variables using discriminant analysis or PCA (Tabachnick and Fidell 1983; Digby and Kempton 1987). These two procedures are often done concurrently and are the objectives of many classification studies.

In this scenario, the exploration of relationships between variables and determining predictive relationships are only as valid as the initial cluster analysis. Cluster analysis algorithms are extremely sensitive to data structure and variable selection with the final cluster solution not robust or invariant to these inputs (Milligan 1996). If the true underlying cluster structure is poorly represented in the groups, then exploring variable relationships that account for group membership becomes problematic.

We propose combining some of the advantages of tree-structured methods with cluster analysis into an approach that forms groups and models group membership. We take advantage of the recursive nature of classification trees to include variable interactions, hierarchical relationships, and reduction of dimensionality while avoiding some of the potential pitfalls of more traditional multivariate techniques.

The objective of this study was to compare a cluster and discriminant analysis approach for lake classification against a tree-structured classification approach with data from Wisconsin lakes. We compared classification methods for their ability to form groups of lakes and classify observations into groups with a high degree of certainty, a necessary requirement if lake classification is to be used in effective management activities. Our approach is intended to graft the useful elements of cluster analysis onto tree-structured methods while seeking to overcome some of the weaknesses inherent to both procedures. Cluster analysis defines groups across a measurement space but is often difficult to interpret because of its multivariate nature. Tree-structured methods require predefined groups and provide great explanatory power in a compact and efficient manner. A procedure that hierarchically forms groups, evaluates the goodness of each split or

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Table 1. Limnological and lake morphometry variables for the 667 lakes used in this study.

	Mean	SE	Minimum	Maximum
Lake area (ha)	141.52	9.247	10.1	1 544.9
Maximum depth (m)	9.23	0.262	1.2	35.7
Drainage basin area (ha)	5582.86	718.142	21.1	196 654.7
Calcium (mg/L)	9.50	0.318	<1.0	45.0
Magnesium (mg/L)	4.20	0.184	<1.0	31.0
Total alkalinity (mg/L)	37.40	1.382	5.0	202.0
Chloride (mg/L)	2.20	0.085	<1.0	31.0
pH	7.13	0.033	5.0	9.6
Total phosphorus (mg/L)	0.031	0.0019	<0.004	0.995
Total nitrogen (mg/L)	0.763	0.0173	0.130	2.840
Nitrogen to phosphorus ratio	34.09	0.734	0.70	79.40
Transparency (m)	2.47	0.063	0.4	8.5
Turbidity (JTU)	2.60	0.116	<0.40	34.00
Chlorophyll *a* (μg/L)	11.54	0.644	<0.50	87.10

group formation, reduces dimensionality, and maintains variable interactions within the hierarchical arrangement or tree would provide a valuable tool for developing classification systems.

Methods and materials

The limnology and lake morphometry data set used to develop classification systems was obtained from Lillie and Mason (1983). These data were collected during 1979 as part of a statewide stratified random lake sampling effort in which 24% of all lakes within each of the 72 counties in Wisconsin were sampled by Wisconsin Department of Natural Resources personnel. This sampling effort was restricted to lakes between 25 and 2000 ha and greater than 0.5 m maximum depth. This resulted in a cross-sectional sample of 673 lakes in northern Wisconsin. Wisconsin, located in the north-central United States, has a defined northern lakes region were 85% of the lakes in the State are located. For the purposes of lake classification, the six lakes and impoundments greater than 12 000 ha were excluded, resulting in a final classification data set of 667 lakes, 542 of which were randomly segregated into a model building data set, while the remaining 125 lakes were retained as a model validation set.

Classification methodology

Two approaches were used to classify Wisconsin lakes. The first relied on traditional multivariate statistical methods including cluster analysis and DFA and was based upon the methodology used to classify Minnesota lakes (Schupp 1992). In this application, lake groups were formed with a *k*-means cluster analysis (Gordon 1981; Digby and Kempton 1987; Milligan 1996) on the limnological variables from the model development data set (Table 1). Once lake groups were constructed, a DFA (Tabachnick and Fidell 1984) was used to develop a classification function to predict lake group membership. In these analyses, data were first standardized to a mean of 0 and variance of 1 because of varying measurement units and scales of the limnological and morphometric data.

The traditional multivariate method was contrasted with a hierarchical classification tree approach. In this method, we propose a lakes classification system based upon modification of hierarchical regression tree modeling outlined by Breiman et al. (1984), Loh and Vanichsetakul (1988), and Loh and Shih (1997). Our method differs from these traditional CART's, however, in that lake group is not known, and making groups, rather than predicting an existing target, is the priority.

The basic techniques employed in our method involved a combination of PCA (Pielou 1984), *k*-means cluster analysis, and multiple logistic regression (Agresti 1996). Multiple logistic regression is similar in paramaterization to the more familiar multiple linear regression. The difference between the two methods is that the target or dependent variable in logistic regression is nondimensional and is often, as in this case, binary events with complementary states, such as dead versus alive, present versus absent, or, more explicitly, lake group 1 versus lake group 2.

Lakes were first clustered into two groups based upon a subset of limnological or morphometric variables. The subset of variables used in the first split corresponded to those variables that had significant ($p < 0.05$) correlations with the first principal component from PCA, thus explaining most of the variation observed within the data set. Each group was subsequently split in a binary fashion into subgroups, which were then subsequently split into smaller subgroups resulting in a dichotomous tree of lake groups. At each branch point, the tree used a different subset of variables for splitting. These variables were selected by conducting PCA on the reduced data set and selecting the variables with the highest correlations with the first principal component.

While lake groups were formed with *k*-means cluster analysis, group membership was modeled using a multiple logistic regression. At each split or branch point the subset of limnological variables used to split the data with *k*-means cluster analysis was used in a stepwise multiple logistic regression. The "best" model was fit based on Akaike information criteria and likelihood ratio test of model deviance using nested models (Agresti 1996). Group membership of individual lakes was calculated as a probabilistic function of this reduced dimension logistic model with assignment to a lake group based upon the calculated probability of group membership. This approach was applied iteratively at each branch in the tree and resulted in a divisive classification tree in which group membership at each branch is a probabalistic function of logistic models (Fig. 1). Branching continues until within-group sample sizes become smaller than the number of independent variables, 15 in this case, or until further splitting results in a degradation of classification efficiency and an increase in misclassification rates.

Misclassification in this study is defined as a lake having a probability of group or class membership less than 0.9. The purpose of this restriction was to conservatively assign correct classification to a given lake. A penalty for a low probability of group membership is desirable if the goal of classification is resource management and the investment of resources into lake groups.

In each classification procedure, the model development data set was used in a resubstitution validation estimate with an observation considered misclassified if its posterior probability of class membership was less than 0.9. The 125 lakes in the validation data set were also used as test sample estimate of classification success.

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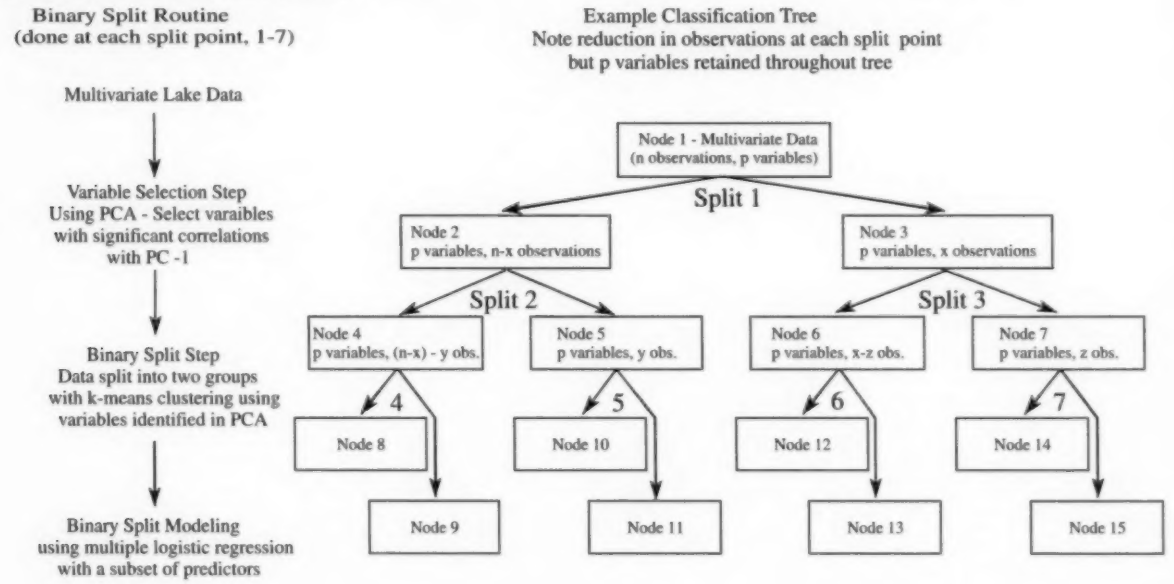
Table 2. Summary of lake characteristics of lake groups formed by cluster and discriminant analysis.

	Cluster 1 (n = 83)	Cluster 2 (n = 361)	Cluster 3 (n = 79)	Cluster 4 (n = 19)
Lake area (ha)	Large (350)	Moderate (200)	Small (80)	Small (40)
Maximum depth (m)	Moderate (7)	Deep (13)	Shallow (5)	Moderate (9)
Drainage basin area (ha)	Large (8100)	Moderate (1020)	Moderate (2440)	Small (204)
Total alkalinity (mg/L)	Moderate (50)	High (80)	Low (15)	Low (18)
pH	Moderate (7.3)	High (7.8)	Low (6.6)	Low (6.8)
Magnesium (mg/L)	Moderate (5)	High (10)	Low (1.8)	Low (1.9)
Calcium (mg/L)	Moderate (11)	High (19)	Low (3.1)	Low (4.2)
Total phosphorus (mg/L)	High (0.070)	Moderate (0.024)	Low (0.009)	Moderate (0.023)
Nitrogen to phosphorus ratio	Low (18)	Moderate (38)	High (128)	Moderate (36)
Transparency (m)	Low (1.1)	High (3.0)	Moderate (2.2)	Moderate (2.5)

Note: Cluster groups with different designations (low, medium, high) are significantly different with one-way ANOVA.

Fig. 1. Example of decision tree showing the binary split routine and how it is applied at each branching point in the tree. Application of the binary split routine results in splitting the data into smaller subsets and variable reduction for predicting group membership. Node and split numbering are identified.



All statistical procedures and algorithms were programed in SAS version 6.12 (SAS Institute Inc. 1990).

Results

Use of *k*-means cluster and DFA for classification

Iterations of the *k*-means cluster algorithm resulted in the selection of four distinct clusters or lake classes (Table 2). The selection of four clusters was based upon examination of the cubic clustering criterion and the adjusted R^2 of each iteration of the clustering algorithm (SAS Institute Inc. 1990). The four-cluster solution was superior to solutions with three or five clusters and slightly better than solutions with six and seven clusters. All solutions greater than seven clusters were less desirable.

The groups produced by the four-cluster solution (Table 2) differ limnologically and morphologically, with differences in cluster groups evident with DFA (overall $F = 83.5$, $p < 0.0001$). An examination of cross-validation results and of the posterior probabilities of correct classification indicated a misclassification rate of 11.6% (Table 3). Of the 88% of lakes correctly classified, 16.8% were classified with a probability of less than 0.90, resulting in an overall error rate of 26.4%. Use of the 125 lakes in the validation data set resulted in an error of classification (probability of less than 0.9) in 28.8% of the lakes.

Building and testing hierarchical classification trees

To build hierarchical classification trees in this example, PCA's of limnological and morphological variables were examined as a starting point for entry of predicator variables into the tree (Table 4). In the first split, five PCA factors explained 76% of the variation in the data set. Correlations of the original variable with the composite factors (factor

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Table 3. Cross-validation results of cluster/DFA for model development data set (542 lakes).

From/to	Cluster 1	Cluster 2	Cluster 3	Cluster 4	Posterior probability less than 0.90	Number misclassified	Total error
Cluster 1	78	0	3	2	26/78	5	31
Cluster 2	27	314	16	4	35/314	47	82
Cluster 3	6	1	71	1	16/71	8	24
Cluster 4	5	0	0	14	3/14	5	8
Total	116	315	90	21	80/477	63	145/542
Error (%)	8.4	12.3	10.1	26.3	16.8	11.6	26.4

Note: Posterior probabilities of group membership less than 0.90 are considered misclassified and contribute to total error. Total error refers to misclassified lakes plus lakes classified with less than 0.9 probability of correct classification.

Table 4. Correlations of the first principal component with the original lake variables along with proportion of variance explained for the six binary splits used in classification.

	Node 1	Node 2	Node 3	Node 4	Node 5	Node 6
Lake area (ha)	0.009	0.717*†	0.681*	–0.144	–0.135	–0.156
Maximum depth (m)	0.093	0.463*	0.691*†	–0.072	0.149	–0.085
Drainage basin area (ha)	0.001	0.603*†	0.586*†	0.154	–0.221	0.207
Calcium (mg/L)	0.952*	0.074	–0.085	–0.151	–0.085	0.316*
Magnesium (mg/L)	0.948*†	0.053	–0.026	–0.058	–0.022	0.272*
Total alkalinity (mg/L)	0.973*†	0.081	–0.095	0.015	–0.019	0.354*
Chloride (mg/L)	0.431*	0.165	–0.033	–0.056	0.191	0.158
pH	0.631*	–0.105	–0.102	0.117	–0.053	0.196
Total phosphorus (mg/L)	0.148	–0.025	0.224	–0.632*†	0.785*†	0.144
Total nitrogen (mg/L)	0.148	–0.234	0.186	0.355*	0.478*	0.121
Nitrogen to phosphorus ratio	–0.058	–0.172	0.455*	0.578*	0.591*	0.165
Transparency (m)	–0.071	0.202	–0.213	–0.623*†	0.402*†	–0.188
Turbidity (JTU)	0.109	–0.125	0.018	0.173	0.190	0.312*
Chlorophyll *a* (μg/L)	0.118	–0.273	–0.054	–0.525*	0.365*	0.286*
% variance explained	32	37	34	29	28	18

*Significant correlations.
†Variables used in the reduced parameter multiple regression models for each split.

loadings) indicated that the first principal component is associated with alkalinity/cation levels. Based upon these correlations, the alkalinity, cation, and pH variables were first used to form dichotomous splits in the data.

After the first split, a separate PCA was conducted on each of the smaller subsets or nodes. For node 2 the PCA found lake and drainage basin area, maximum depth, and water transparency to be significantly correlated with factor 1. For node 3, lake and drainage basin area, maximum depth, and nitrogen to phosphorus ratios had significant correlations. For each node, these variables were used to produce binary splits with *k*-means cluster analysis. Each binary split was then modeled using stepwise multiple logistic regression, further reducing the number of predictor variables necessary to accurately place lakes into groups.

In splitting node 2, for example, lake and drainage basin area, maximum depth, and water transparency were used to produce the binary split. However, only lake area and drainage basin area were necessary to predict group membership in the multiple logistic regression. Results of the PCA's and the multiple logistic regressions by node are shown in Table 4.

The first split resulted in an inability to classify 10 of the 542 lakes into one of two groups based upon magnesium and alkalinity (Fig. 2). The second split (split of node 2) based upon drainage basin area and lake area in node 2 and maximum depth and drainage basin area in node 3 resulted in 26 lakes not classifiable at this split, or a cumulative error rate of 6.6% after two branches in the tree (or formation of four lake groups). A third level of branching based upon water clarity, total phosphorus, chlorophyll, and nitrogen resulted in a large increase in the misclassification rate (24.4% after three splits with seven lake groups versus 5.7% with four lake groups). Examination of individual splits at the third level indicated that the split of nodes 4 and 5 resulted in a further misclassification of only 13%. A split of node 6 had a 37% rate of misclassification. Due to low sample size (10 lakes), node 7 was not split into smaller subgroups. Based upon this loss of efficiency and small sample sizes, the tree was pruned after the second split for the right side of the tree. All three splits on the left side of the tree gave reliable classification and were retained (Fig. 3). Subsequent splits of nodes 8 and 9 resulted in a misclassification rate of 42% and were not retained.

This resulted in a lake classification composed of six lake groups that were different in terms of lake chemistry and morphometry (Table 5). Applying the multiple logistic regression models developed with the tree to the 125-lake validation data set resulted in a misclassification of 12 of the 125 lakes or a rate of 9.6%. Application of the discriminant

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Fig. 2. Cross-validation tree showing branches and pruned tree. At the third level of splitting the misclassification rate becomes large on the right side of the tree, indicating that six lake groups is the appropriate stopping point for classification. Final lake groups are shown as rectangles.

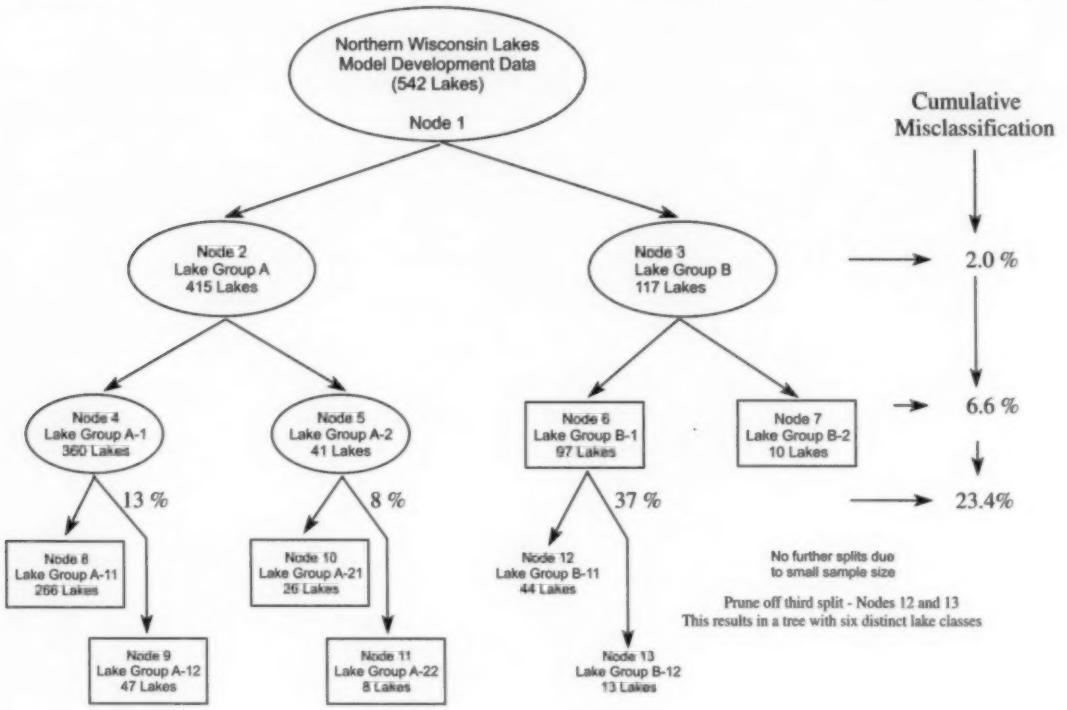

Fig. 3. Final decision tree with approximate decision points and node descriptions. Final lake groups are shown as rectangles. TP, total phosphorus; DBA, drainage basin area; Trans, transparency. See Table 1 for units.

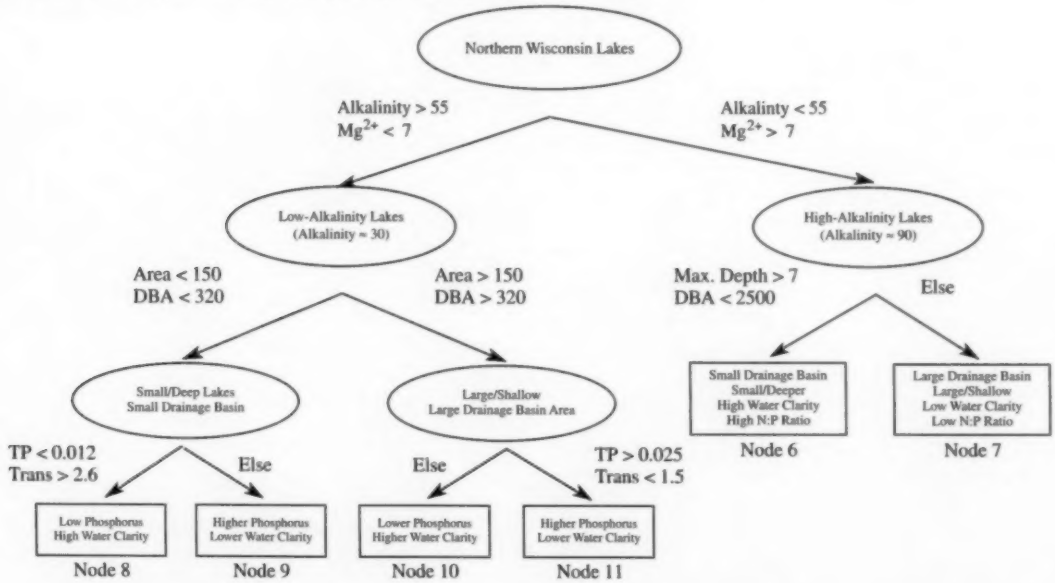

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Table 5. Summary of lake characteristics of lake groups formed by decision tree.

	Node 6 (n = 97)	Node 7 (n = 10)	Node 8 (n = 266)	Node 9 (n = 47)	Node 10 (n = 26)	Node 11 (n = 8)
Lake area (ha)	Small (130)	Large (925)	Small (85)	Small (131)	Moderate (332)	Large (518)
Maximum depth (m)	Deep (14)	Shallow (6)	Moderate (11)	Deep (17)	Moderate (10)	Shallow (7)
Drainage basin area (ha)	Moderate (1940)	Large (19851)	Small (179)	Small (227)	Moderate (1387)	Moderate (4572)
Total alkalinity (mg/L)	High (90)	High (108)	Low (20)	Low (22)	Low (28)	Low (32)
pH	High (7.5)	High (7.8)	Low (6.8)	Low (6.7)	Low (6.9)	Low (6.9)
Magnesium (mg/L)	High (12)	High (10)	Low (2.0)	Low (2.9)	Low (3.5)	Low (2.9)
Calcium (mg/L)	High (22)	High (21)	Low (5.5)	Low (7.2)	Low (8.1)	Low (8.5)
Total phosphorus (mg/L)	Moderate (0.028)	High (0.072)	Low (0.008)	Moderate (0.016)	Moderate (0.017)	High (0.061)
Nitrogen to phosphorus ratio	High (38)	Low (18)	High (44)	Moderate (28)	Moderate (31)	Moderate (24)
Transparency (m)	High (2.8)	Low (1.3)	High (3.1)	Moderate (2.2)	High (2.8)	Low (1.7)

Note: Lake groups with different designations (low, medium, high) are significantly different with one-way ANOVA.

function classification equation to the same data set resulted in an error rate of 28.8% (Table 6).

Discussion

The results of this study indicated that the application of tree-structured methods to classification problems in ecology may be fruitful. The classification algorithm used in this example had three beneficial outcomes not typically available in cluster analysis and DFA. First, the development of a decision tree resulted in an accurate and simple classification function that is hierarchical in nature and efficiently classifies new observations not used in tree construction. This was evident in the classification of the 125 lakes in the validation data set where the decision tree method was approximately three times more accurate in classifying new observations than the DFA. That DFA would have difficulty classifying observations not used in model development has been previously reported (Verbyla 1987).

Second, the final classification tree also reduced the dimensionality of the classification question. The original data set contained 15 variables, all of which were used to develop the branches and binary splits within the tree. The actual modeling of group membership with multiple logistic regression, however, used only seven of the 15 original variables. This has real implications in the data requirements necessary to classify new lakes. The tree-structured approach employed in our example uses the power of all variables to form groups but predicts group membership using only a small subset at each binary split. In this example, collection of only seven limnological variables would be needed to place a lake into a class.

Finally, tree-structured methods are able to incorporate both variable interactions and different variable relationships existing in different areas of the measurement space. This was evident in our example where low-alkalinity lakes formed one branch of the tree and high-alkalinity lakes the other. This first split essentially partitioned the sampling space into two distinct subspaces. The subsequent split of each branch was then independent of the other with different variables or different break points for common variables responsible for separation and modeling of group membership.

For example, in low-alkalinity lakes the second split was a function of drainage basin and lake area whereas in high-alkalinity lakes the second split resulted from drainage basin area and maximum lake depth. Both branches used basin area but with different values for the splits (320 versus 2500 ha, respectively). The other variables used to predict group membership on each branch also differed, indicating that variables had different relationships in different areas of the measurement space. Furthermore, even the simple tree portrayed in our study included the interaction between basin area and alkalinity with both low and high alkalinity occurring with small drainage basins.

The inclusion of variable interactions and using different models in different partitions of the measurement space are a powerful consequence of tree-structured classification. Both the improved classification efficiency and the reduction of dimensionality demonstrated in this example were probably a result of these properties. Instead of modeling the discrimination plane(s) as a linear combination of variables, we are

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Table 6. Comparison of cross-validation results of both classification methods using the 125-lake validation data set.

Cluster/DFA lake groups	Number of lakes	Misclassifed	Classification tree lake groups	Number of lakes	Misclassified
Cluster 1	20	9	Node 6	23	2
Cluster 2	78	18	Node 7	2	0
Cluster 3	21	7	Node 8	69	6
Cluster 4	6	5	Node 9	18	2
—	—	—	Node 10	11	1
—	—	—	Node 11	2	1
Total	125	36		125	12
Error rate (%)		28.8			9.6

Note: These data were not used to develop classification models. The decision tree classification had a misclassification rate approximately one third of the cluster/DFA method.

incorporating nonlinearity and allowing the discrimination plane to bend and curve with the data (Vanichsetakul 1986). This results in more accurate and interpretable classification with fewer variables, as was evident in our classification of northern Wisconsin lakes.

The cluster/DFA method resulted in four distinct lake classes whereas the tree method was able to achieve a finer resolution of classification with six lake classes. Finer resolution of classification may be attained in the cluster/DFA method, but the misclassification rate is likely to be higher than that observed in the four-class model. The fine resolution of the classification with small error becomes important when examining the variables that produced the observed binary splits and applying classification to a potential management scenario such as development of lake riparian zones and land use decisions.

Some of the classification splits used parameters that are relatively conservative, changing slowly over time and relatively unaffected by either management or land use changes. Other splits used parameters that are potentially useful for improving our understanding of and capability to predict consequences of land use decisions in a subset of lakes. Specifically, the terminal splits on the left side of the tree that produced nodes 8–11 were driven by phosphorous and water transparency. These parameters are known to be sensitive to changes in land use and nonpoint inputs as well as to influence the production of biological communities (Jennings et al. 1999). Modeling of biological interactions within these lake classes can allow prediction of community composition given alternative land use scenarios. This might be applied to predicting biological responses to degradation in the watershed or, alternatively, to predicting the outcome of proposed restoration.

The model of northern Wisconsin lakes presented represents classification at one scale. The development of classifications at various scales of resolution would also be beneficial, especially for application of lake classes to management questions. Models developed within watersheds, for example, may provide better predictions of a biological response such as walleye (*Stizostedion vitreum*) reproductive status or population estimates of individual species whereas classifications conducted across watersheds may provide better information on how land use patterns influence limnological and biological interactions.

This study represents a novel statistical approach to the old question of classification in ecology and aquatic sciences. The algorithm is not completely refined and the assessment of model fit somewhat ad hoc. Simulation studies to determine the behavior of the algorithm with a variety of data distributions and better methods of optimizing hierarchical splits would result in a more cohesive and generalizable method and provide a better assessment of model fit. What is evident, however, is the utility of the hierarchical approach to complex multivariable ecological classification questions.

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Behavioural and metabolic effects of chronic exposure to sublethal aluminum in acidic soft water in juvenile rainbow trout (*Oncorhynchus mykiss*)

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Abstract: Triplicate groups of 15 softwater-acclimated juvenile rainbow trout (*Oncorhynchus mykiss*) were randomly allocated to one of three treatments: pH 6.5 with no aluminum, pH 5.2 with no aluminum, and pH 5.2 with 30 μg labile aluminum·L^{-1}. The aluminum dose was sublethal and continued for 34 days. Treatment effects on swimming behaviour, metabolism, feeding, food conversion efficiency, and blood parameters were determined. Fish exposed to aluminum displayed hypoactivity that was statistically distinct from both control groups from day 1 onwards. Exposure to acid alone elicited no behavioural effects. There were no significant differences in metabolic rates between the treatment groups. Feeding rates of the fish exposed to aluminum became depressed, reaching a minimum on day 15, and gradually recovered thereafter, but never to the preexposure levels. Swimming behaviour was a more sensitive index of exposure to aluminum than feeding. Fish exposed to aluminum had significantly fewer red blood cells and lower haematocrit than the controls, indicating haemodilution. Aluminum is known to act as a respiratory toxicant, restricting aerobic scope. In addition, these data suggest that fish respond to aluminum exposure by reducing metabolically costly activities such as routine swimming behaviour to allow for the increased maintenance costs associated with acclimation and damage repair.

Résumé : Nous avons soumis en les choisissant au hasard trois groupes de 15 truites arc-en-ciel (*Oncorhynchus mykiss*) juvéniles acclimatées à l'eau douce aux trois traitements suivants : pH 6,5 sans aluminum, pH 5,2 sans aluminum et pH 5,2 avec 30 μg aluminum labile·L^{-1}. La dose d'aluminum était sous-létale et les poissons y ont été exposés durant 34 jours. On a déterminé les effets du traitement sur la nage, le métabolisme, l'alimentation, l'efficacité de la conversion des aliments et des paramètres sanguins. Les poissons exposés à l'aluminum ont montré une hypoactivité qui les distinguait statistiquement des deux groupes témoins, à partir du premier jour et jusqu'à la fin de l'expérience. L'exposition à l'acidité seule n'a pas eu d'effet sur le comportement. On n'a observé aucune différence significative entre les taux métaboliques des trois groupes. Les taux d'alimentation des poissons exposés à l'aluminum ont d'abord chuté pour atteindre un minimum au jour 15, et ont ensuite augmenté sans jamais atteindre cependant les niveaux pré-exposition. Le comportement natatoire était un indice plus sensible de l'exposition à l'aluminum que l'alimentation. Par rapport aux témoins, les poissons exposés à l'aluminum renfermaient significativement moins de globules rouges et leur hématocrite était inférieur, ce qui témoigne d'une hémodilution. On sait que l'aluminum est toxique pour le système respiratoire en ceci qu'il réduit la capacité aérobie. En outre, ces données montrent que les poissons réagissent à l'exposition à l'aluminum en réduisant leurs activités coûteuses sur le plan métabolique, comme les déplacements ordinaires, pour compenser les coûts d'entretien accrus liés à l'acclimatation et à la réparation des dommages.

[Traduit par la Rédaction]

Introduction

Acid deposition, principally as a consequence of the combustion of fossil fuels, is a serious pollution problem in the Northern Hemisphere. If acidity is deposited onto sensitive soils with poor buffering capacity, trace metals including aluminum may be mobilised. Low environmental pH alone (pH 4.7–5.5) is not acutely toxic to salmonids (Reader et al. 1989; Rosseland et al. 1990). However, low pH in combination with aluminum in soft water poses a serious threat to all aquatic organisms and has been cited as the main cause of fish kills in acid waters (Kelso et al. 1986; Howells et al. 1990; Rosseland et al. 1990). The principal organ that is adversely affected by exposure to acid and aluminum is the gill. Fish exposed to acid and aluminum are known to suffer respiratory stress (Meuller et al. 1991; Wilson et al. 1994*b*) and ionoregulatory and osmoregulatory dysfunction (McDonald and Milligan 1988; McDonald et al. 1991).

Wilson et al. (1994*a*) exposed juvenile rainbow trout (*Oncorhynchus mykiss*) to a sublethal concentration of aluminum (30 μg·L^{-1}) in acidic soft water (pH 5.2) and found that although fish experienced a dramatic reduction in appetite

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Table 1. Measured values (means ± SEM) for water chemistry parameters.

Parameter	6.5/0	5.2/0	5.2/Al
pH	6.4±0.02	5.1±0.03	5.3±0.03
Al ($\mu g \cdot L^{-1}$)	1.9±0.3	1.9±0.3	29.2±1.1
Ca^{2+} ($\mu mol \cdot L^{-1}$)	18.5±0.5	20.9±0.6	22.2±0.9
Mg^{2+} ($\mu mol \cdot L^{-1}$)	34.9±0.9	37.1±0.9	36.7±0.9
Na^{+} ($\mu mol \cdot L^{-1}$)	52.6±2.3	53.0±1.8	50.9±1.9
K^{+} ($\mu mol \cdot L^{-1}$)	28.4±1.0	32.8±1.0	33.7±1.0

Note: In the acidic pH control (5.2/0) and acid and aluminum exposed (5.2/Al) treatments, n = 108. For the neutral pH control (6.5/0) treatment, n = 88. Labile aluminum in aluminum-dosed tanks averaged 99.4% of total aluminum dosed (±0.61 SEM, n = 12).

(>90%) during the first 7 days of exposure, they paradoxically doubled their food conversion efficiency (FCE) (percentage of food consumed converted into dry mass gain). As in other studies (Freeman and Everhart 1971; Schofield and Trojnar 1980), it was anecdotally noted that fish exposed to aluminum were less active. It was hypothesised that a reduction in activity may permit a greater proportion of the energy consumed to be diverted to growth. Behaviour is a sensitive and environmentally relevant measure of exposure to metals that may reflect changes in "Darwinian fitness" (Depledge et al. 1995). The study described here used analysis of sensitive patterns of swimming behaviour, coupled with metabolic rate determinations, to determine if changes in behaviour and metabolic rate could account for the diversion of a greater proportion of energy to growth in response to exposure to aluminum.

Materials and methods

Animal holding

Triploid juvenile rainbow trout between 13 and 28 g were obtained from Wilmington trout farm, Wilmington, Devon, U.K., and were held in a flow-through system of dechlorinated tap water for 1 week before undergoing a progressive transfer to artificial soft water (ASW) over a 5-day period (nominal ion concentrations (micromoles per litre) in the ASW were 15 Ca^{2+}, 60 Na^{+}, 35 Mg^{2+}, and 25 K^{+}). ASW was obtained by adding appropriate amounts of $CaCl_2 \cdot 2H_2O$, NaCl, $MgSO_4$, and KOH to reverse osmosis and deionised water (Elgastat Prima 7 system, Elga Ltd., High Wycombe, U.K.). Fish were held in the ASW at 15°C and pH 6.5 for 3 weeks before the start of baseline determinations. A photoperiod of 12 h light : 12 h dark was used throughout.

Following softwater acclimation, groups of 15 fish were randomly allocated to nine circular grey tanks containing 20 L of ASW. Water in each tank was aerated using an air stone. Grey tanks were chosen to permit as close to natural behaviour as possible to be observed under laboratory conditions (Fanta 1995). The tanks were circular with no distinctive markings to avoid the establishment of territories by the fish and excessively aggressive behaviour. Tanks were then randomly allocated to one of three treatments: circumneutral pH (6.5) with no added aluminum (6.5/0), acidic pH (5.2) with no added aluminum (5.2/0), and acidic pH (5.2) with 30 μg aluminum$\cdot L^{-1}$ added (5.2/Al). Each tank received 0.15 L ASW$\cdot min^{-1}$ (i.e., 10.8 volume replacements$\cdot day^{-1}$). On day 6 of the exposure, it was necessary to remove five fish, selected at random, from each tank because the stocking density was too high to permit satisfactory control of the water pH at the flow rate of 0.15 L$\cdot min^{-1}$. The mean pH of the mean for the acidic tanks during the initial 6 days of the exposure was 5.5 ± 0.07 SEM.

Water for the acidic treatments was acidified using a pH controller (Hanna H18710E, Hanna Instruments Ltd., Leighton Buzzard, U.K.) and low-conductivity pH electrode (Russell CT711/LCW, Russell pH Ltd., Fife, Scotland). Acidification was achieved using a 4:3 N mix of sulphuric to nitric acid, which represents the current proportions of acid deposition in the United Kingdom as estimated by EMEP (1996). Aluminum concentrations were elevated to the appropriate level using a stock solution of aluminum chloride ($AlCl_3 \cdot 6H_2O$) dosed via a peristaltic pump. Vigorous aeration of the ASW in all tanks ensured equilibration with atmospheric carbon dioxide.

Water cation levels were monitored on a daily basis using atomic absorbtion spectrophotometry (Pye Unicam SP9, Pye Unicam Ltd., Cambridge, U.K.), and independent checks of water pH were made (Hanna H18314 pH meter and a Russell CT711/LCW low conductivity electrode; details as before). Periodically during the baseline and daily during exposure to aluminum, water aluminum concentrations were measured using the pyrocatechol violet method as described by Dougan and Wilson (1974). Labile aluminum was also determined by filtering water samples through a Whatman 0.45 μm filter paper and passing it through a column of Amberlite™ ion-exchange resin (Table 1).

Feeding regime and growth measurements

Prior to the start of the exposure, fish were fed to satiation every second day on a diet of Trouw Excel 2.3 slow-sinking pellets (Trouw UK Ltd., Preston, U.K.). Small aliquots of food were offered at regular intervals until unconsumed pellets were observable at the base of the tanks 2 min after the previous aliquot had been offered. The time taken to reach satiation was recorded. Any pellets remaining in the tank after satiation were removed using a siphon and the number of pellets recorded. An equivalent number of dry pellets were then added back to the container and the mass of food consumed calculated for each tank.

A feeding regime whereby the fish were fed to satiation every second day was adopted to minimise any complications due to the specific dynamic action (SDA) affecting the metabolic rate measurements. These were taken on the afternoon of the day following a feeding event (27 h postfeeding) to ensure that the peak of the SDA had passed (Jobling 1983). Feeding every second day is known not to affect food conversion efficiencies (Teskeredzic et al. 1995). Growth rates were assessed every 8 days by removing individual fish from the experimental tanks, gently blotting on a cotton towel, and weighing in a tared vessel containing the appropriate exposure water. Fish length was measured at the same time. Fish were then returned to the appropriate experimental tanks.

Exposure to aluminum has previously been shown to cause a severe reduction in appetite, e.g., to about 10% of preexposure levels (Wilson et al. 1994*a*). To ensure that food conversion efficiencies and metabolic rate measurements were directly comparable between treatments, it was decided to feed all fish the same equivalent ration (grams of food per gram wet weight of fish) as the lowest feeding group (i.e., the fish exposed to aluminum). Therefore the quantity of food offered to the controls was the equivalent (grams of food per gram wet weight of fish) of the mean satiation ration in the lowest feeding treatment.

Metabolic rate determinations and behavioural measurements

On days –16, –14, –8, –4, 0, 1, 2, 3, 4, 8, 12, 18, 20, 26, and 32, oxygen consumption rates (M_{O_2}) were determined during daylight hours, 27 h postfeeding, concurrently with the behavioural measurements. These measurements were taken to represent routine metabolic rate.

A closed respirometry design was used. The M_{O_2} was determined using an oxygen meter and electrode (Strathkelvin models 781 and 1302, respectively, Strathkelvin Instruments, Glasgow,

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Scotland). During M_{O_2} determinations the aeration of and water supply to the tanks were stopped and an air- and water-tight seal formed on the top of the tanks using a clear perspex lid and inflatable O-ring. Once the seal was formed, animals were allowed to settle for a period of 10 min before measuring the change in water oxygen partial pressure (P_{O_2}) over a 20-min period. Water P_{O_2} was never allowed to fall below 70% saturation. The oxygen consumption per wet mass of fish (millimoles of oxygen per kilogram per hour) was estimated using linear regression of the fish mass between each weighing interval. Blank M_{O_2}'s for the tanks were made in the absence of the fish on the days when fish were weighed. These measurements were consistently less than 1% of the lowest M_{O_2} recorded in the presence of fish.

During the respirometry measurements, fish activity was recorded using a JVC video recorder (HR-J635EK, JVC (UK) Ltd., London, U.K.) and a Watec video camera fitted with a 12-mm television lens (Video Controls Ltd., Runcorn, U.K.). To minimise disturbance to the fish and for ease of movement between the tanks, the camera was mounted on a pulley system suspended above the tanks. The experimental area was shielded from the rest of the aquarium using black plastic curtains.

During behavioural monitoring, each tank was filmed for about 4 min, and 2-min portions of the video recordings from each tank were later analysed for three mutually exclusive and distinct measures of swimming behaviour: slow swimming, position holding, and burst episodes. Slow swimming was defined as swimming movements estimated to be less than two body lengths per second using low-frequency and low-amplitude movements of the tail to propel the fish. Position holding was when the fish maintained a stationary position in the tank, predominantly by using skulling movements of the pectoral fins. Burst activity was defined as rapid movements estimated to be at speeds of greater than two body lengths per second using high-frequency and high-amplitude movements of the tail. Such activity was usually associated with aggressive social interactions and typically lasted for less than 0.5 s. The behaviour of five fish in each tank was analysed. The fish were selected using a random number generator to produce X,Y coordinates. These were then transcribed to a transparency and placed over the monitor screen. The behaviour of the fish closest to these coordinates at the start of the analysis period was then monitored and quantified. A mean value was then calculated for each of the three replicate tanks in each treatment ($n = 3$).

Terminal sampling

At the end of the exposure period, all fish were sacrificed by a swift blow to the head. A mixed arteriovenous blood sample was taken by caudal puncture using a heparinised needle (3060 USP units sodium heparin·mL^{-1}). Haematocrit was determined using heparinised haematocrit tubes centrifuged at 10 000 rpm for 5 min. Haemoglobin content was assayed using a micromodification of the cyanmetheamoglobin method (Sigma kit 525-A, Sigma-Aldrich Co. Ltd., Poole, U.K.). Blood suspensions were made by diluting blood 1:200 in a solution of physiological saline with 4% gluteraldehyde. Five counts of red blood cells (RBC's) per sample were made using a haemocytometer. The remaining blood was centrifuged at 10 000 rpm for 4 min and the plasma decanted for plasma glucose concentration determinations (Boehringer Mannheim Glucose/GOD-Perid® method, Boehringer Mannhiem, Lewes, U.K.).

Calculations

Condition indices (CI's) were calculated as

$$\text{CI} = \text{weight(g)/length}^3\text{(cm)}.$$

Food conversion efficiencies were calculated as described by Brett and Groves (1979) using the fish dry mass gain (assuming dry mass = 27% of wet weight, Wilson et al. 1994*a*) divided by dry mass of food consumed and expressed as a percentage. The M_{O_2} was calculated under static conditions. Oxygen consumption per wet mass of fish was calculated thus:

$$M_{O_2}\ (\text{mmol } O_2 \cdot \text{kg}^{-1} \cdot \text{h}^{-1}) = (\Delta P_{O_2\ \text{fish}} - \Delta P_{O_2\ \text{blank}}) \times \alpha_w O_2 \times V/(M \times t)$$

where $\Delta P_{O_2\ \text{fish}}$ is the change in water P_{O_2} (millimetres of mercury) over a specified time with the fish present and $\Delta P_{O_2\ \text{blank}}$ is the change in water P_{O_2} over a specified time with the fish absent, $\alpha_w O_2$ is the solubility of oxygen in water at 15°C (millimoles of oxygen per litre per millimetre of mercury) (Boutilier et al. 1984), V is the tank volume (litres), M is the mass of the fish (kilograms), and t is time (hours). The mean corpuscular haemoglobin content (MCHC) was calculated by division of the haemoglobin content by the haematocrit value expressed as a decimal.

Statistical analysis

Statistical significance at $p < 0.05$ for each variable was tested using a nested design ANOVA. As the data for slow swimming and position holding were expressed as percentages, it was necessary to arcsine transform the data to achieve a normal distribution and homogeniety of variance. Scheffe's post hoc test was used to calculate contrast coefficients in order to detect treatment differences.

Results

Mortality

There were no mortalities in the 5.2/Al tanks throughout the study, proving that a dose of 30 μg aluminum·L^{-1} was truly sublethal. Similarly, there were no mortalities in the 5.2/0 tanks. One of the 6.5/0 groups did suffer a fungal infection, however, and between days 15 and 16, five fish died. It was decided to kill the remaining fish in this tank, as the social structure of the population would have been disrupted by the mortalities, possibly influencing behavioural patterns. Data presented for the 6.5/0 groups after day 16 therefore represent the mean of two rather than three tanks. We are confident that the fungal infection was restricted to this one tank, as there were no signs of fungal infection among the other fish, appetite remained keen in the controls, and there were no further mortalities.

Feeding, growth, and FCE

Prior to the start of the exposure, all groups had similar feeding rates of between 2.75 and 3.75% body weight·day^{-1}. Exposure to aluminum induced a reduction in appetite that was slow initially. The feeding rate dropped below preexposure levels on day 7, rapidly falling thereafter, reaching a minimum level on day 15 (Fig. 1). From this point onwards, all groups expressed some recovery of appetite; however, there were marked differences in the degree of recovery between the replicate tanks of fish exposed to aluminum, ranging from about 15 to 90% of preexposure feeding rates.

Growth was similar in all treatments throughout the study (Fig. 2). When fed the same ration, all groups grew at similar rates, despite large differences in behavioural patterns observed. The increase in size of the error bars in the aluminum-exposed groups after day 15 reflects the differential recovery of feeding and therefore growth between tanks of the same treatment.

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Fig. 1. Food consumption in the replicate tanks of fish exposed to aluminum. Each line represents the food consumed by a replicate tank (n = 1): open circles, replicate 1; half-solid circles, replicate 2; solid circles, replicate 3. The mean value, shown by the solid line only (n = 3), represents the mean satiation ration consumed by the 5.2/Al groups and therefore the ration offered to the two control treatments (5.2/0 and 6.5/0). Time zero represents the point where the treatments were initiated.

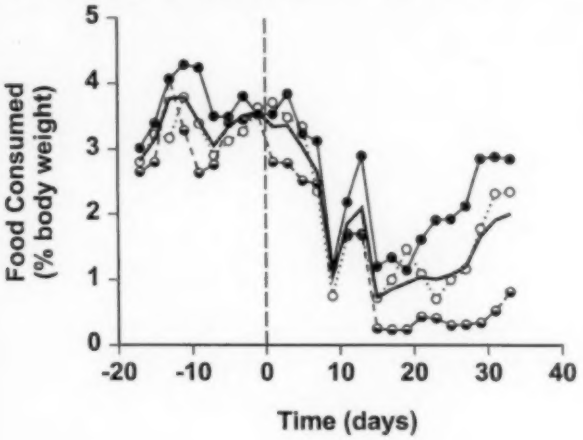


Fig. 2. Mean body weight of groups of fish in each treatment against time. Solid triangles, mean growth rate of the groups of fish exposed to aluminum (5.2/Al); open triangles, mean of the 5.2/0 groups; open diamonds, mean of the 6.5/0 groups. Error bars represent the mean SEM's of the 5.2/Al groups only, which increase in magnitude throughout the study as a greater differential in feeding rates between the replicates was expressed. The SEM's (n) on day 34 for the control groups were ±1.6 (30) for 5.2/0 and ±2.2 (19) for 6.5/0. The mean ration consumed by all treatments is included as a reference.

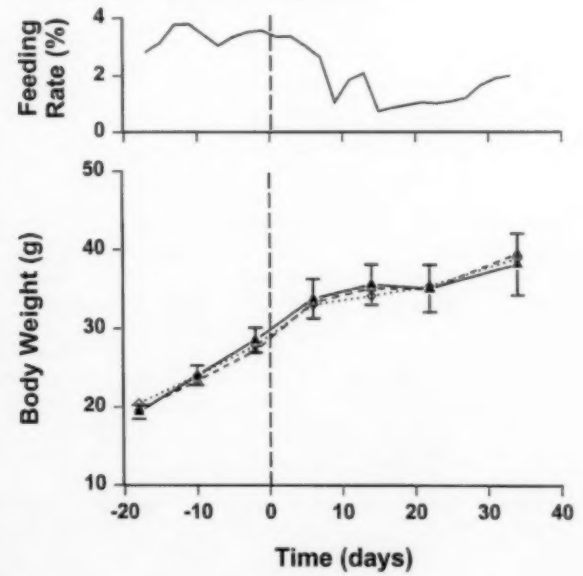
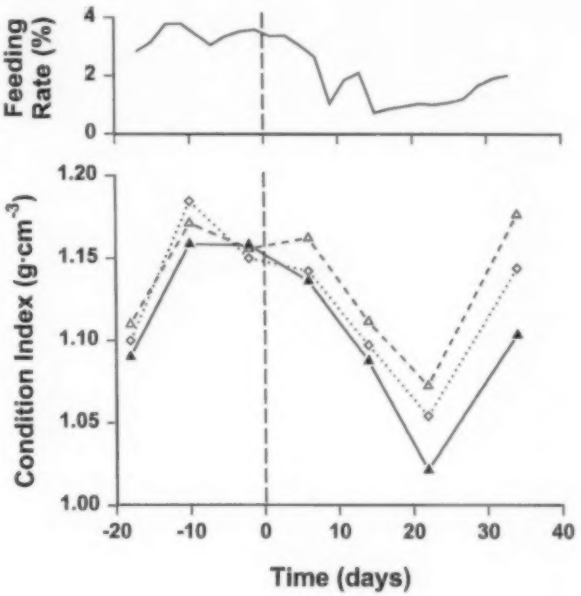


Fig. 3. Mean CI's for groups of fish in each treatment. Solid triangles, mean CI of the groups of fish exposed to aluminum (5.2/Al); open triangles, mean of the 5.2/0 groups; open diamonds, mean of the 6.5/0 groups. Information on the mean ration consumed is included for reference. All groups reach a minimum value at the measurement period immediately after the lowest feeding point. The SEM's (n) for the groups on day 34 were ±0.02 (30) for 5.2/Al, ±0.02 (30) for 5.2/0, and ±0.02 (19) for 6.5/0.



The CI's of the fish (Fig. 3) closely followed the feeding trends, reaching a minimum value on day 22, the measurement point immediately after the period when the lowest feeding rates were recorded. The CI of all fish then showed recovery to day 34. The CI's of the fish exposed to aluminum were the lowest of all groups throughout the exposure, but they were not significantly different from the controls at any point.

During the exposure, no differences in FCE were recorded. The FCE's of the fish exposed to aluminum tended to be lower than in the control groups during the first 22 days of the study, but these differences were not significant (Fig. 4). The negative FCE's between days 14 and 22 corresponded to the period of time when food intake rates were at their lowest. From day 14 to 22 the ration fed was close to maintenance for the two control groups. The large error bars for the FCE of the fish exposed to aluminum reflect the differential recovery of feeding and growth between the replicates.

Metabolic rate and behaviour

There were no significant differences between the metabolic rates of fish in any of the treatments (Fig. 5). The metabolic rates of all groups fell after the beginning of the exposure, reached a minimum at day 19, and gradually increased thereafter. This paralleled changes in the feeding re-

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Fig. 4. Mean FCE and SEM for groups of fish in each treatment. Solid bars, mean of the 5.2/Al groups; hatched bars, mean of the 5.2/0 groups; open bars, mean of the 6.5/0 groups. The period of lowest FCE coincides with the period of lowest CI's (Fig. 3) and growth rates (Fig. 2). There were no significant differences between the treatments at any point.

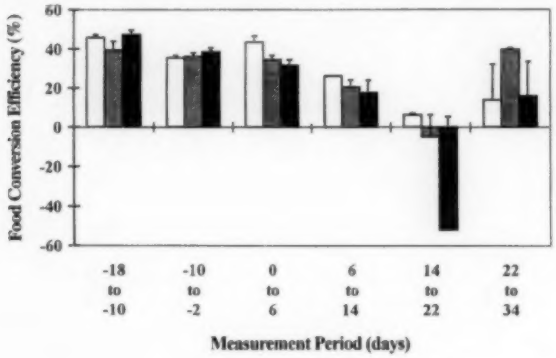


Fig. 5. Mean Mo_2 for groups of fish in each treatment (n = 3). Solid triangles, mean Mo_2 of the groups of fish exposed to aluminum (5.2/Al); open triangles, mean of the 5.2/0 groups; open diamonds, mean of the 6.5/0 groups. The mean ration consumed is included for reference. The Mo_2's fell when the ration consumed was reduced, and gradually recovered after day 17 when the ration fed increased. There were no significant differences between the treatments at any point during the experiment. Error bars are not shown for reasons of clarity; however, the mean SEM's were ±0.92 for 5.2/Al, ±0.96 for 5.2/0, and ±0.68 for 6.5/0.

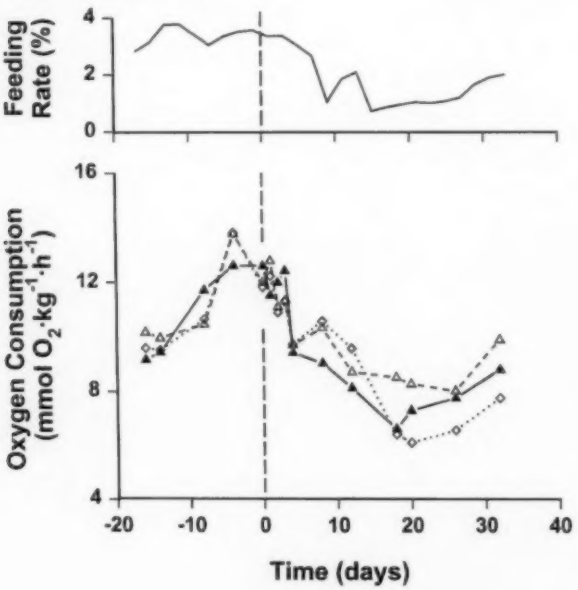
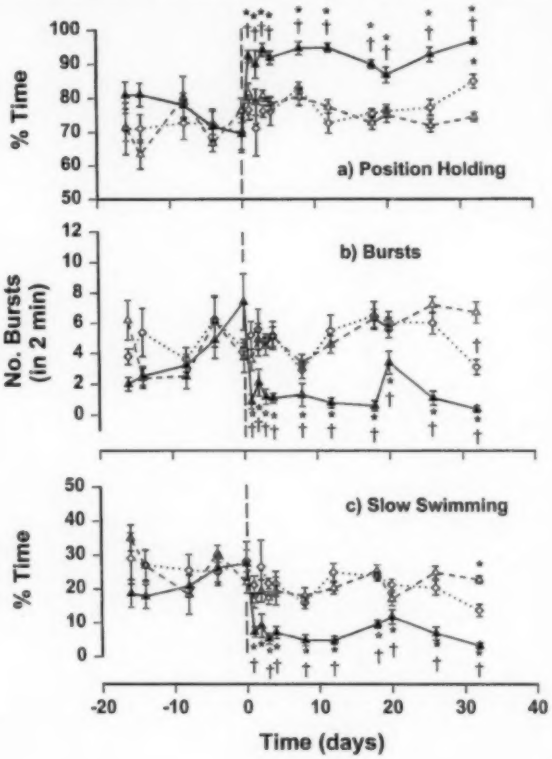


Fig. 6. Mean swimming behaviours and SEM's of groups of fish in each treatment: (*a*) position holding, (*b*) burst-swimming episodes, and (*c*) slow swimming. Solid triangles, mean of the groups of fish exposed to aluminum (5.2/Al); open triangles, mean of the 5.2/0 groups; open diamonds, mean of the 6.5/0 groups. Swimming behaviours were measured over 2-min periods. Each data point represents the mean of the three replicates of each treatment. Error bars represent the mean SEM of the three replicate values. An asterisk denotes significant difference from the 6.5/0 groups at $p < 0.05$ and a dagger denotes significant difference from the 5.2/0 groups at $p < 0.05$.



sponse, probably as metabolic rate is closely correlated with ration fed (Jobling 1981).

The swimming behaviour of the fish exposed to aluminum exhibited dramatic changes upon the initiation of the exposure. From day 1, fish exposed to aluminum became significantly less active ($p < 0.05$) and remained so throughout the duration of the exposure, irrespective of the measure of swimming behaviour employed (Fig. 6). The fish exposed to aluminum spent greater than 90% of their time position holding, whereas the control groups routinely spent around 75% of their time position holding (Fig. 6*a*). The number of burst-swimming episodes observed was dramatically reduced in the fish exposed to aluminum (Fig. 6*b*). The mean number of burst-swimming events recorded in a 2-min period for the aluminum-exposed fish was usually less than two, whereas for the controls, it was greater than five. Figure 6*c* shows the slow-swimming data, which are the mirror image of the position-holding data (Fig. 6*a*). Fish exposed to aluminum typically spent less than 10% of their time slow swimming

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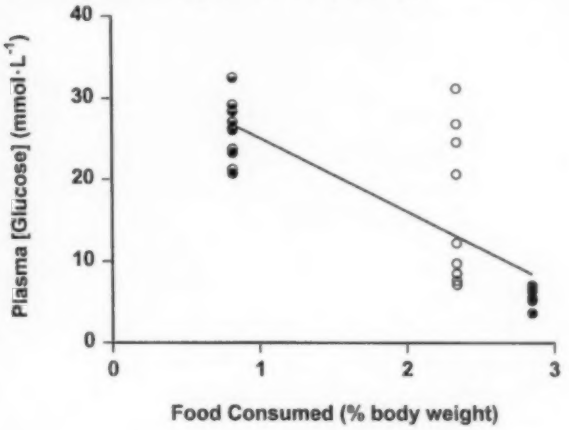
Table 2. Values for the haematological parameters measured upon terminal sampling on day 34.

Parameter	6.5/0	5.2/0	5.2/Al
Haematocrit (%)	27.3±1.1 (18)	27.1±0.7 (27)	24.6±0.9*† (30)
Haemoglobin ($g \cdot dL^{-1}$)	6.78±0.27 (19)	6.02±0.37 (30)	5.76±0.34* (30)
RBC counts ($10^6 \cdot mm^{-3}$)	0.56±0.02 (11)	0.62±0.02 (21)	0.44±0.02*† (20)
MCHC ($g \cdot dL^{-1}$)	25.0±1.5 (17)	22.5±1.0 (27)	23.5±1.2 (30)

Note: Values quoted are the means for each treatment ± SEM (n in parentheses). Statistical significance: *significantly different from the 6.5/0 treatment at $p < 0.05$; †significantly different from the 5.2/0 treatment at $p < 0.05$.

Fig. 7. Plasma glucose concentrations in individual fish in each aluminum-exposed replicate. Open circles, replicate 1; half-solid circles, replicate 2; solid circles, replicate 3. The regression line is plotted through the mean values for each replicate, indicating a linear relationship between the food consumption of the group and the mean plasma glucose concentration. The mean values and SEM's for the 5.2/0 and 6.5/0 treatments were 8.03 ± 0.51 and 6.75 ± 0.08 mmol glucose·L^{-1}, respectively.



compared with about 25% in the controls. This highlights the sensitivity of swimming activity as a response to exposure to aluminum.

Terminal sampling

The fish exposed to aluminum showed profound haematological disturbances, having significantly reduced haematocrit, haemoglobin content, and RBC counts (Table 2). The MCHC was not significantly different in the fish exposed to aluminum from those in the controls. Plasma glucose levels for individual 5.2/Al fish from all three replicate tanks are shown in Fig. 7. When a regression line is plotted through the tank mean values, a linear inverse relationship with appetite is revealed. The fish in the 5.2/Al replicate with the lowest feeding rate had the highest plasma glucose concentrations. Conversely, those with the highest feeding rate had the lowest plasma glucose concentrations. The mean plasma glucose values and SEM's for the 6.5/0 and 5.2/0 treatments were 6.75 ± 0.08 and 8.03 ± 0.51 mmol glucose·L^{-1}, respectively.

Discussion

Mortality, feeding, and growth

Exposure to 30 μg aluminum·L^{-1} was truly sublethal, with no deaths recorded over 34 days. However, exposure to aluminum clearly depressed appetite, although this took longer to reach a minimum level than previously recorded (15 days as opposed to 2 days recorded by Wilson et al. 1994*a*). All three replicates of the aluminum-exposed fish demonstrated some degree of subsequent feeding recovery, but this was not homogeneous. One group nearly recovered to the preexposure levels, one group remained very depressed throughout (about 15% of former levels), and the third group exhibited an intermediate degree of recovery. The mean ration fed to the control groups of fish was therefore very similar to that fed to the intermediate-recovered group of 5.2/Al fish.

It was noteworthy that an inverse linear relationship existed between the plasma glucose concentrations and the feeding rates of the replicate 5.2/Al tanks when a regression line was plotted through the mean plasma glucose levels recorded in each replicate 5.2/Al group (Fig. 7). It is commonly believed that the control of food intake is under multifactoral control (Fletcher 1984), with a number of variables including chemosensory stimuli, stomach expansion, hormones, and plasma metabolites contributing to that control. Hyperglycemia is a known secondary stress response (Wedemeyer et al. 1990) and can act as an appetite depressor (Kuzmina 1966; Bellamy 1968), reducing the ration required to reach satiation. We propose that the sixfold elevation in plasma glucose levels measured in the lowest feeding group of fish exposed to aluminum could have acted as a strong satiation signal. This is reinforced by the fact that the fish had lower than the preexposure or even negative FCE's while apparently satiated. Interestingly, the fish with the intermediate degree of recovery had a much greater spread of plasma glucose concentrations. It is tempting to speculate that the fish with the lowest plasma glucose concentrations in this replicate tank may have had the greatest appetite among the group and therefore consumed the majority of the ration fed. It is well known in aquacultural practices that the introduction of fish that are feeding to a group of nonfeeding fish encourages the nonfeeding fish to feed (Stirling 1977). Recovery of feeding response during exposure to aluminum and the rate of this apparent recovery may therefore be dictated by social groupings. For example, if one fish experiences appetite recovery, the rest of the cohort in the tank are also likely to recover. It is possible that the group of fish with the lowest plasma glucose levels had acclimated to aluminum exposure, wheras the other two groups were still undergoing acclimation processes. This theory is further reinforced by the fact that there were no differences in the water chemistry between the replicate tanks of the fish exposed to aluminum. In particular, there were no differences in the water chemistry parameters pertinent to aluminum toxicity, namely pH, aluminum, and calcium concentrations.

As all control groups were fed a ration equivalent to the

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mean of the 5.2/Al groups once the exposure began, all groups of fish showed similar growth rates, with small increases in mass measured for all groups up until day 14. From day 14 to 22, when the lowest ration was fed, both the 5.2/0 and the 5.2/Al groups actually lost weight. The low ration consumed was therefore below maintenance in these groups. The CI's of the fish exposed to aluminum tended to be the lowest throughout the exposure, reaching a minimum value at day 22, the measurement point immediately after the period of lowest feeding rate. However, at no point were the CI's of the 5.2/Al groups significantly different from those of the controls.

The FCE of all groups decreased as the ration fed was reduced. Some recovery of FCE was evident after the ration improved, but there were large variations within the replicates of the 6.5/0 and 5.2/Al treatments during this period. There was no dramatic increase in FCE, as previously found in fish exposed to aluminum (Wilson et al. 1994*a*). This is a more conventional response for exposure to a toxicant than that observed by Wilson et al. (1994*a*), as exposure to aluminum is clearly having a "loading" effect on metabolism (Brett 1958). That is, exposure to aluminum increases the "cost" of maintenance. This is likely to be due to the induction of damage repair mechanisms and acclimatory responses, allowing less of the energy consumed to be utilised for the purposes of growth.

Behaviour and metabolism

Exposure to aluminum clearly had a profound effect on swimming behaviour, inducing hypoactivity that was significantly different from that of the controls from day 1 throughout the exposure. The behavioural effects were consistent throughout the exposure period. Fish exposed to aluminum spent significantly less time swimming, more time stationary, and displayed fewer burst-activity episodes (Fig. 6). Swimming at speeds of greater than two body lengths per second involves significant recruitment of white muscle fibres in teleost fish (Jayne and Lauder 1994). Use of white anaerobic muscle incurs an oxygen debt and is therefore very metabolically costly (anaerobic metabolism releases only 7% of the free energy available from glucose as opposed to 93% during aerobic metabolism, Duncan and Klekowski 1975). These data imply that the fish exposed to aluminum were unwilling or unable to support the use of the white muscle mass and are perhaps further evidence of a trade-off in the energy requirements of damage repair mechanisms reducing the apparent scope for activity. These observations follow the same trends as those anecdotally observed by Freeman and Everhart (1971), Schofield and Trojnar (1980), Ogilvie and Stechey (1983), and Wilson et al. (1994*a*). Similarly, Cleveland et al. (1986) and Smith and Haines (1995) observed that early life stages of brook trout (*Salvelinus fontinalis*) and Atlantic salmon (*Salmo salar*) exposed to aluminum in acidic soft water were less active. The present study reports the first detailed quantification of alterations in different swimming behaviours of juvenile rainbow trout over a chronic exposure period. There were significant differences between the swimming behaviour of the 6.5/0 and 5.2/0 treatments at only one point during the exposure. Thus, sublethal acid exposure alone (pH 5.2) had little or no measurable effect on swimming behaviour. Interestingly, despite differential levels of recovery in the feeding and plasma glucose responses of the different replicate tanks of fish exposed to aluminum, there were no distinct differences measured in the swimming behaviour of these replicates.

There was a trend for reduced oxygen consumption in all treatments from day 0 to 17. This closely followed the trends shown in ration consumed and probably represents a decreased amount of energy being required for food processing and assimilation despite the fact that the Mo_2 measurements were made 19 h after peak Mo_2 normally associated with the SDA.

Adopting a feeding regime whereby fish in all treatments were fed the same equivalent ration allowed direct comparison of metabolic rates. There were no significant differences between the routine Mo_2's in any of the treatments on any one day, even though it was clear that the fish exposed to aluminum were quantifiably less active. Since activity is known to be a large and variable part of the routine metabolic rate (Koch and Weiser 1983; Boisclair and Tang 1993), it would appear that routine metabolic rate was maintained by forfeiting routine swimming activity levels. This further supports the theory that aluminum was exerting a loading influence on metabolism. Thus the predicted loading influence of aluminum exposure on metabolism was revealed, but only when the changes in routine activity rates were taken into account. The loading effect of exposure to aluminum on metabolic rate was possibly due, at least partly, to the processes required to repair gill damage. Thus the proportion of the metabolic scope available for other metabolic processes such as locomotor activities may be reduced. The feeding regime also revealed that under nutritional stress, the swimming behaviour of the control fish was unchanged, whereas there was a significant reduction in the swimming activity of the fish exposed to the additional stressor of aluminum.

Gill damage due to exposure to aluminum reduces apparent surface area and affects ion and gas transport (Wood et al. 1988; Wilson et al. 1994*b*). The activity of the fish may well be limited by their compromised ability to extract oxygen from water. This is reinforced by data that demonstrated that fish exposed to aluminum in acidic soft water had impaired maximum aerobic swimming speeds and a 30% reduction in maximum Mo_2 ($Mo_{2\,max}$) (Wilson et al. 1994*b*). In the present study, routine Mo_2's averaged about 9 mmol $O_2 \cdot kg^{-1} \cdot h^{-1}$. The Mo_{2max} values reported by Wilson et al. (1994*b*) for similar sized rainbow trout exposed to 30 μg aluminum$\cdot L^{-1}$ was about 14 mmol $O_2 \cdot kg^{-1} \cdot h^{-1}$ as opposed to about 21 mmol $O_2 \cdot kg^{-1} \cdot h^{-1}$ for control fish. Clearly the fish exposed to aluminum in the present study would have a reduced scope for aerobic activity due to a reduced differential between the routine Mo_2 and the Mo_{2max}.

Blood analysis

The haematological data present further evidence for the impaired respiratory scope of the fish exposed to aluminum. The 5.2/Al treatment group had significantly reduced haematocrit and RBC counts than both of the control groups and a significantly lower haemoglobin concentration than the 6.5/0 treatment. This is indicative of haemodilution, which would reduce the blood oxygen-carrying capacity and potentially compromise the aerobic capacity of the fish exposed to aluminum. The MCHC's of the treatments were not signifi-

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cantly different, indicating that although the RBC's of fish in each treatment had the same heamoglobin content, there were significantly fewer RBC's to transport oxygen in the fish exposed to aluminum.

Conclusions

The paradoxical doubling of FCE of fish exposed to aluminum reported by Wilson et al. (1994*a*) was not observed in the present study. The improved feeding technique, whereby all fish were fed the same equivalent ration as the lowest feeding group, ensured that FCE, growth, and Mo_2 measurements were directly comparable and lead us to conclude a more conventional picture of a loading factor on metabolism.

Behavioural analysis in this study proved to be the most sensitive indicator of exposure to aluminum, with significant hypoactivity observed from day 1 throughout the study in all swimming behaviours analysed. Behaviour represents an integrated, whole-organism response to aluminum exposure whereby the sum total of many biochemical and physiological events produced a sensitive tertiary stress response of ecological relevance. We propose that one mechanism that could explain the aberrations in swimming behaviour could be the reduced capacity of the fish to extract oxygen from water due to physical damage to the gill. This would be compounded by osmoregulatory and ionoregulatory dysfunction, coupled with changes in haematological status, which would impair oxygen delivery to tissues.

The data described here confirm the previously predicted loading effects and costs of exposure to a toxicant. In the laboratory, fish were fed to satiation, a situation that is unlikely to occur in wild populations, especially as acidic waters are known to have lower invertebrate productivity levels (Ormerod et al. 1989). If native populations of fish exposed to aluminum experience changes in routine swimming behaviour similar to the laboratory fish, then it is likely to affect their ability to forage for the limited food available, avoid predation, migrate, and successfully reproduce.

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Mechanisms underlying amphipod responses to zebra mussel (*Dreissena polymorpha*) invasion and implications for fish–amphipod interactions

María J. González and Amy Downing

Abstract: We examined mechanisms underlying increased amphipod abundance after zebra mussels (*Dreissena polymorpha*) invaded Lake Erie. We conducted field substrate preference experiments to test the hypotheses that amphipods prefer (*i*) high-complexity substrates over low-complexity substrates and (or) (*ii*) substrates with high mussel feces and pseudofeces deposition over substrates with low deposition. We measured amphipod preference for bare rock, live mussels, and dead mussels in spring (May 1996) and summer (July and August 1995, June and August 1996). Habitat complexity affected amphipod habitat preference, and preference varied seasonally. In spring, amphipod density was highest on dead mussels, but the response was highly variable. In midsummer (June and July), amphipods showed no substrate preference. In late summer (August), amphipods consistently preferred high-complexity mussel substrates. Amphipods never preferred low-complexity substrates. We also evaluated effects of zebra mussel presence on fish–amphipod interactions in laboratory feeding trials. We tested the hypothesis that mussel presence decreases bluegill (*Lepomis macrochirus*) and yellow perch (*Perca flavescens*) predation on amphipods. Predation by bluegill but not yellow perch was significantly lowered by mussel presence. Our results support the hypothesis that the increase in amphipods upon zebra mussel invasion is due to increased habitat complexity, possibly by reducing predation risk. However, the effects of zebra mussel on fish–amphipod interactions depended on predator species.

Résumé : Nous avons étudié les mécanismes responsables de l'accroissement de l'abondance des amphipodes après l'invasion du lac Érié par la moule zébrée (*Dreissena polymorpha*). Nous avons réalisé des expériences de terrain sur les préférences des amphipodes en matière de substrat pour tester les hypothèses suivant lesquelles ces derniers préféreraient (*i*) les substrats complexes aux substrats simples et (ou) (*ii*) les substrats comportant de grandes quantités de fèces et de pseudo-fèces de moules aux substrats comportant de faibles quantités de ces dépôts. Nous avons mesuré l'affinité des amphipodes pour la roche nue, les moules vivantes et les moules mortes au printemps (mai 1996) et à l'été (juillet et août 1995, juin et août 1996). Les préférences des amphipodes en matière d'habitat étaient fonction de la complexité de l'habitat, et elles variaient selon les saisons. Au printemps, la densité des amphipodes était le plus élevée sur les moules mortes, mais la réponse était très variable. Au milieu de l'été (juin et juillet), les amphipodes n'ont pas montré de préférence. À la fin de l'été (août), les amphipodes ont régulièrement préféré les substrats de moules complexes. Les amphipodes n'ont jamais préféré les substrats simples. Nous avons aussi évalué les effets de la présence de moules zébrées sur les interactions entre poissons et amphipodes dans des essais d'alimentation en laboratoire. Nous avons testé l'hypothèse que la présence des moules entraînerait une réduction de la prédation des amphipodes par le crapet arlequin (*Lepomis macrochirus*) et la perchaude (*Perca flavescens*). La prédation par le crapet arlequin, mais pas celle par la perchaude, a diminué de façon significative en présence de moules. Nos résultats confirment l'hypothèse que l'accroissement de l'abondance des amphipodes par suite de l'invasion du milieu par la moule zébrée est lié à l'accroissement de la complexité de l'habitat, qui aurait peut-être pour effet de réduire les risques de prédation. Cependant, les effets de la présence de moules zébrées sur les interactions entre poissons et amphipodes dépendaient de la nature du prédateur.

[Traduit par la Rédaction]

Introduction

Several studies have shown evidence of a major diversion of energy from pelagic to benthic habitats upon invasion of zebra mussels (*Dreissena polymorpha*) in the Great Lakes. Increased flux of particulate matter from the water column to the lake bottom (Klerks et al. 1996) and increased water clarity have occurred following zebra mussel invasions (Fahnenstiel et al. 1995). Water column chlorophyll concentration and phytoplankton abundance (Holland 1993; Nicholls and Hopkins 1993) have declined in some areas, while macrophytes and benthic algae have increased due to increased

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light penetration after mussel invasion (Lowe and Pillsbury 1995; Skubinna et al. 1995; Stuckey and Moore 1995). Intermediate trophic levels of benthic and pelagic communities have also responded to zebra mussel invasion. Rotifer and copepod abundances have declined after the mussel invasion in some areas (e.g., Lake Erie, MacIssac et al. 1995), while the biomass of benthic invertebrates has increased on bedrock substrates (Dermott et al. 1992; Stewart and Haynes 1994; Ricciardi et al. 1997). Amphipod abundance in particular has drastically increased and amphipods have become one of the dominant components of the benthic invertebrate community (Dermott et al. 1992; Stewart and Haynes 1994; Ricciardi et al. 1997). Increased amphipod abundance following zebra mussel invasion in the Great Lakes can have important implications for fish populations. Amphipods are food items for several species of commercial and recreational value in the Great Lakes, such as yellow perch (*Perca flavescens*) (Hayward and Margraf 1987; Roseman et al. 1996), walleye (*Stizostedion vitreum*) (Mathias and Li 1982), and bluegill (*Lepomis macrochirus*) (Crowder and Cooper 1982; Mittelbach 1988). In this paper, we explore the mechanisms underlying the response of amphipods to the zebra mussel invasion as well as the implications of their response for upper trophic levels, namely fish.

Several possible mechanisms have been suggested to explain the high abundance of amphipods in zebra mussel beds. Mussel colonies provide higher structural complexity than bare rocks. Therefore, amphipods may increase due to increased habitat complexity (Dermott et al. 1992). Another potential mechanism is that food availability is higher in mussel colonies than on bare rocks because of biodeposition of seston converted to mussel feces and pseudofeces. It is possible that amphipods select a habitat with high deposition rates (Walz 1978; Dermott et al. 1992). It is also possible that both increased habitat complexity and increased food availability are responsible for increased amphipod abundance in mussel beds. We conducted a field experiment to test the role of increased habitat complexity and food availability provided by zebra mussels in controlling amphipod abundances. We measured amphipod preference among substrates varying in habitat complexity (bare rocks versus zebra mussel colonies) and biodeposition (live zebra mussels versus dead zebra mussels) under in situ conditions. A higher number of amphipods in the mussel treatments (live and dead) than in the bare rock treatment supports the hypothesis that amphipods prefer high habitat complexity. A greater amphipod density in live than in dead mussel colonies supports the hypothesis that nutritional enhancement plays a role in habitat preference by amphipods. Habitat preference may vary seasonally due to changes in food availability and predation risk (Gilinsky 1984; Luecke et al. 1990). Therefore, we performed experiments in late spring and early and late summer.

An increase in amphipods could have a positive impact on fish populations by increasing food resources. On the other hand, habitat complexity provided by zebra mussels can also reduce amphipod predation risk. Several studies have shown that increased habitat complexity causes a decline in fish predation rates on invertebrates (Gilinsky 1984; Heck and Crowder 1991; Diehl 1993). Although amphipod abundance may increase in the presence of zebra mussels, fewer amphipods may actually be available to fish predators due to the increase in spatial refugia provided by the mussel colonies. In this study, we evaluated the effect of zebra mussels on fish–amphipod interactions by measuring predation rates of yellow perch and bluegill on amphipods in the presence and absence of mussels under laboratory conditions. Yellow perch is an important species in commercial fisheries in the Great Lakes. Bluegill is a major component of lakes and reservoirs that potentially could be invaded by zebra mussel. We hypothesized that fish predation rates would be lower in treatments with zebra mussels than in treatments without zebra mussels because mussel colonies provide spatial refugia from predators.

Methods

Field experiments: amphipod substrate preference

We conducted five field experiments at Hatchery Bay, South Bass Island, in the western basin of Lake Erie to document seasonal habitat preference of amphipods under natural conditions. The experiments were conducted in mid-July and early August 1995 and mid-May, early June, and early August 1996. Water surface temperature was 11–15°C in the spring experiment (May 1996) and 21–25°C in the summer experiments (June, July, and August).

Experimental design

Four types of substrates were used in this experiment: (*i*) bare rocks, (*ii*) rocks with dead zebra mussels, (*iii*) rocks with live zebra mussels, and (*iv*) no rocks (control). The bare rock and live and dead mussel substrates consisted of rocks collected in Lake Erie. The live mussel treatment contained mussels naturally attached to rocks. The dead mussel substrates were constructed by gluing empty mussel shells with epoxy putty (Z*spar, A-788 splash zone compound) onto rocks in the place where live mussels had once been attached. Thus the dead and live zebra mussel treatments had similar structure and appearance. The base of each empty mussel was glued to the rock area and the valves of each mussel were also glued together to avoid an increase in surface area relative to the live mussel substrate. Previous to the experiment, dead mussel substrates were incubated in the lake for 7–10 days to allow some periphyton growth.

To conduct the experiment, the substrates were rinsed free of fauna and incubated inside plastic cages (22 × 22.5 × 22.5 cm) covered with 1-cm mesh to exclude potential fish predators. The control treatment consisted of empty cages. We used three rocks per cage in the 1995 experiments and two rocks per cage in the 1996 experiments. The number of replicates varied among experiments because some cages were accidentally lost, but there were always four or five replicates per treatment. Scuba divers positioned the cages in two rows anchored to cinder blocks submerged at 5 m depth on substrates consisting of cobbles with mussels and fine sediments. We conducted a preliminary experiment to determine the necessary incubation period. In the preliminary experiment, 12 cages, each with three mussel colonies devoid of fauna, were incubated for a total of 10 days. We retrieved two cages every 2 days and counted the number of amphipods. The number of amphipods colonizing the substrates reached asymptotic values after 6 days of incubation. Therefore, we incubated cages for 7 days in all experiments.

After 7 days, divers collected the substrates by placing the cages in cloth bags and transporting them to the laboratory in less than 2 h. All organisms present on the substrate were immediately removed by shaking the rocks inside a bucket with Lake Erie water for at least 25 min. Organisms were concentrated using a 100-μm sieve, preserved using 10% formalin, and counted using a stereo-

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scopic microscope. To correct for the cage effect, the mean number of amphipods in the control treatment (empty cages) was calculated and subtracted from the total number of amphipods in each cage of the other treatments.

When we processed our samples, we assumed that all amphipods were *Gammarus fasciatus* (Say). Recent studies, however, have reported the presence of an exotic gammarid, *Echinogammarus ischnus* (Stebbing), morphologically very similar to *Gammarus*, associated with zebra mussel colonies (Witt et al. 1997; Dermott et al. 1998). Because we did not distinguish between the two species, we categorize all organisms simply as "amphipods".

To express amphipod abundance in the treatments as amphipods per square centimetre, we calculated the total surface area (TSA) available to amphipods in each treatment. In the bare rock treatment, we assumed that the total rock surface area was available to amphipods. In the dead mussel treatment, we glued the mussel bases to the rocks; therefore the mussel base surface (SA_{base}) and the rock surface to which they were glued (ZSA_{rock}) were not available to the amphipods. Thus, we calculated the available surface area as $TSA_{dead} = NZSA_{rock} + (SA_{zebra} - SA_{base})$, where $NZSA_{rock}$ is the rock surface area not overlain by mussels and SA_{zebra} is the surface area of the zebra mussel shells.

Physical examination of rock with live mussels collected from the lake showed that, unlike dead mussels, the mussel base was not completely attached to the rock. The small spaces in between mussel bases and rocks could provide substantial surface area for amphipods. Therefore, we assumed that in the live mussel treatment, only half of SA_{base} and ZSA_{rock} were available to the amphipods due to the presence of byssal threads. Thus, $TSA_{live} = NZSA_{rock} + 1/2 \cdot ZSA_{rock} + (SA_{zebra} - 1/2 \cdot SA_{base})$.

We used an aluminum foil wrapping technique to determine the total surface area of the bare rocks and the $NZSA_{rock}$ and ZSA_{rock} in the mussel treatments. We used a foil surface area (SA_{foil}) versus foil weight (W_{foil}) regression to estimate the surface area from the weight of the foil. To calculate the surface area provided by mussels, we measured the total length of 135 mussels (size range = 0.5–25 mm). We estimated the weight of foil necessary to wrap each of these mussels (ZW_{foil}) and their base (BW_{foil}) and constructed total length (TL) – weight regressions ($ZW_{foil} = 0.008 \cdot TL^2 + 0.003 \cdot TL$, $r^2 = 0.97$; $BW_{foil} = 0.0004 \times 10^{(0.75 \cdot TL)}$, $r^2 = 0.98$). In each experiment, we measured the total length of each mussel on substrates and calculated ZW_{foil} and BW_{foil} using total length – weight regressions. These foil weights were then used in weight – surface area regressions to calculate all surface areas (NZSA, ZSA, SA_{zebra}, and SA_{base}).

We compared habitat complexity among substrates using a ratio of surface area to volume displacement (*S/V*) (Coull and Wells 1983) in all experiments except July 1995. Volume displacement decreases as interstitial space increases. A higher *S/V* indicates a more complex habitat. In all experiments, mussel substrates had significantly higher *S/V* than the bare rock ($p < 0.01$, one-way ANOVA). Dead and live mussels had a similar *S/V* (Tukey–Kramer test). We assumed that food resource availability was higher in the live mussel substrate than in the other treatments due to the accumulation of feces and pseudofeces produced by zebra mussels. We based this assumption on the different deposition rates observed by Klerks et al. (1996) between dead and live mussel colonies in western Lake Erie. Stewart et al. (1998) also showed a higher accumulation of organic matter in live than in dead mussels and bare rocks in Hatchery Bay, Lake Erie, during summer 1995.

We observed differences in macrophyte growth between rows of cages. Therefore, in the statistical analyses, we tested for block effects (differences between rows). If no significant block × treatment interaction was detected, we pooled the interaction and the residual sum of squares and used it as the appropriate error term for testing treatment effects (Snedecor and Cochran 1989). We tested for differences in total surface area among treatments using two-way ANOVA, blocking for row effect (SAS Institute 1990). We tested for treatment effects (substrate) and seasonal differences (date of experiment) in amphipod density (amphipods per square centimetre) using a three-way ANOVA, blocking for row effects (SAS Institute 1990). A significant date × substrate interaction was detected, indicating that substrate preference varied seasonally (among the different experiments). Therefore, we further tested for substrate and block effects in each experiment using a two-way ANOVA. We used a Tukey–Kramer test to compare the means in the surface area and amphipod density analysis. Amphipod density data were log transformed prior to statistical analysis to meet assumptions of homogeneity of variance.

Laboratory experiments: mediation of fish–amphipod interactions by zebra mussels

Laboratory experiments were performed at the F.T. Stone Laboratory, Hatchery Bay. We measured predation rates of juvenile yellow perch and bluegill on amphipods in the presence and absence of zebra mussels. The average total length was 170 ± 30.8 (SE) mm for bluegill and 130 ± 6.7 mm for yellow perch. Fish were acclimated to the laboratory for 1–2 weeks in a flow-through system using water from Lake Erie and fed with amphipods. The fish were starved for 24 h prior to each feeding trial.

Treatments consisted of 80-L aquaria containing four bare rocks or four rocks with zebra mussel colonies and Lake Erie water. Mean surface area provided by the substrate (bare rocks = 828 ± 31.3 cm^2 or rock with mussels = 750 ± 123 cm^2) was not significantly different among treatments ($t = 0.63$, df = 2, $p = 0.59$). A feeding trial consisted of four aquaria, two replicates per treatment. One hundred and fifty amphipods were added to each tank, and after 20 min, one fish was added. After 6 h, fish were removed from the aquaria and the remaining amphipods were counted. Amphipod density used in the trials was within the range observed in the lake (bare rocks = 0.18 ± 0.007/cm^2 or rock with mussels = 0.20 ± 0.03/cm^2) and was similar between treatments ($t = 0.72$, df = 2, $p = 0.54$). We performed feeding trials during the day (12:00–18:00) and during the night (00:00–06:00). We used 20 bluegill (five day and five night feeding trials) and 16 yellow perch (four day and four night feeding trials). We allowed at least a 24-h period between day and night trials. The number of remaining amphipods per aquarium was analyzed using two-way ANOVA (SAS Institute 1990) to test for substrate effect (bare rock versus mussels colonies) and time effect (day versus night).

Results

Field experiments: amphipod substrate preference

Surface area

We detected significant differences in surface area among treatments in all the experiments. The surface area was significantly higher in the live mussel substrate (1205 ± 63 cm^2) than in the dead mussel (599.5 ± 19 cm^2) and bare rock (549.6 ± 20 cm^2) substrates in July 1995 ($F_{2,10} = 69.1$, $p = 0.0001$). We detected significant differences among all treatments in August 1995 ($F_{2,9} = 60.9$, $p = 0.0001$). Surface area was highest in the dead mussel treatment (1118 ± 48 cm^2), intermediate in the live mussel treatment (898 ± 65 cm^2), and lowest in the bare rock treatment (315 ± 7 cm^2). No significant block or substrate × block interaction effects were detected in either 1995 experiment. We observed a significant substrate × block interaction in May 1996 ($F_{2,6} = 6.6$, $p = 0.02$), indicating that surface area was smaller in the live mussel treatment (448 ± 56 cm^2) than in the dead mussel (659 ± 14 cm^2) and bare rock (739 ± 22 cm^2) treatments in

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Fig. 1. Density (±SE) of amphipods in substrate preference experiments during (*a*) July 1995, (*b*) August 1995, (*c*) May 1996, (*d*) June 1996, and (*e*) August 1996. Error bars that are not apparent are smaller than the symbols. Same letters indicate no significant differences among means using a Tukey–Kramer test.

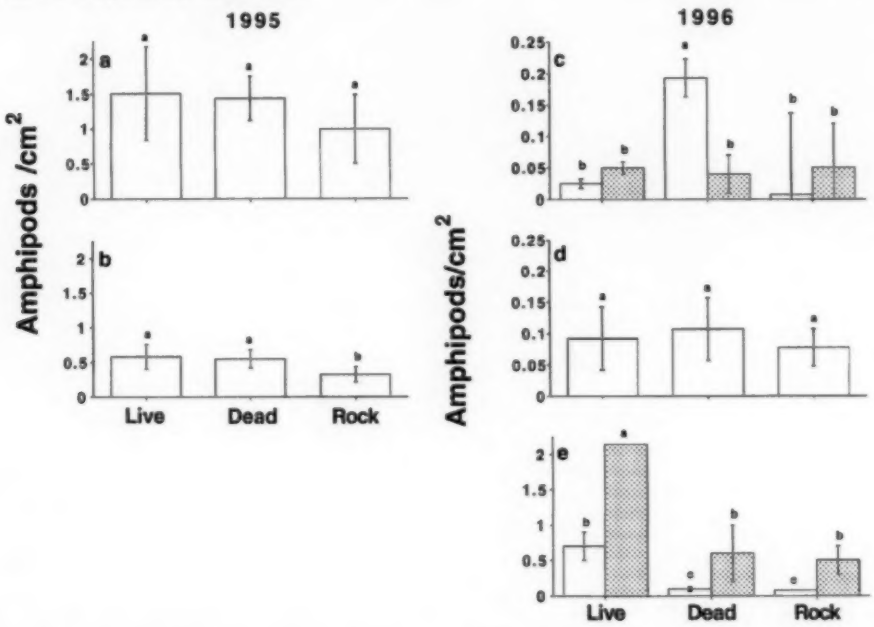

Table 1. Three-way ANOVA on ln(amphipods/cm^2) from habitat preference experiments in the field.

	df	MS	*F* test	*p* value
Date	4	1.13	50.39	0.0001
Block	1	0.03	1.41	0.2431
Substrate	2	0.19	8.27	0.0012
Date × block	8	0.11	4.88	0.0005
Date × substrate	4	0.11	4.80	0.0035
Block × substrate	2	0.02	0.83	0.4444
Date × block × substrate	8	0.02	0.97	0.4752
Error	34	0.02		

block 1. There were no differences in block 2 (live mussels, 607 ± 4 cm^2; dead mussels, 670 ± 14 cm^2; bare rock, 772 ± 10 cm^2). The live mussel substrate had significantly smaller surface area (510 ± 30 cm^2) than the other substrates in June ($F_{2,8}$ = 97.4, p = 0.0001) and August ($F_{2,8}$ = 98.03, p = 0.0001) 1996. Surface area was significantly greater in the bare rock treatment (892 ± 18 cm^2) than in the dead mussel treatment (766.5 ± 7 cm^2) in June. Surface areas were similar in these two treatments in August (871 ± 9 and 845 ± 8 cm^2).

Amphipod density

Significant date × substrate and date × block interactions indicated seasonal differences in amphipod habitat preference (Table 1). Separate analysis of each experiment showed that amphipods preferred high-complexity substrates over bare rocks in late summer (August) experiments. In both 1995 experiments, amphipods density was higher in both mussel treatments than in the bare rock treatment (Figs. 1*a* and 1*b*). However, this trend was only statistically significant in August (Table 2). Substrate × block interactions were not significant in either 1995 experiment.

Amphipod responses in 1996 were more complex than in 1995. In the May experiment, we detected significant treatment effect and block × treatment interaction. Amphipod density was significantly higher in the dead mussel treatment than in the other treatments in block 1 (Table 2; Fig. 1*c*). No significant block × treatment interactions were detected in June and August 1996. Amphipod density was similar among treatments in June (Table 2; Fig. 1*d*), indicating a lack of substrate preference. In August 1996, the number of amphipods that colonized the substrates was higher than in May and June but similar to the mean density in the August 1995 experiment. Amphipod density was higher in the live mussel treatment than in the other treatments. A significant block effect indicated that although the direction of the response was similar in both blocks, the magnitude of the response in block 2 was greater than that in block 1 (Table 2; Fig. 1*e*).

Laboratory experiments: mediation of fish–amphipod interactions by zebra mussels

The presence of zebra mussels affected predation rates of bluegill and yellow perch on amphipods differently. Bluegill predation rate (number of amphipods eaten per fish per hour) was significantly lower in the presence of zebra mussels (p = 0.0027; Fig. 2*a*) during the daytime and nighttime experiments. Yellow perch predation rates were similar in the presence and absence of zebra mussels (p = 0.9798; Fig. 2*b*) during the daytime and nighttime experiments. Bluegill showed significantly higher predation rates during night trials than

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Table 2. Two-way ANOVA on ln(amphipods/cm^2) from habitat preference experiments in the field.

	df	MS	*F* test	*p* value
July 1995				
Substrate type	2	0.08	1.63	0.24
Block	1	0.15	3.31	0.11
Error	10	0.049		
August 1995				
Substrate type	2	0.043	4.57	0.04
Block	1	0.008	0.89	0.37
Error	8	0.009		
May 1996				
Substrate type	2	0.008	6.91	0.02
Block	1	0.0003	0.29	0.61
Substrate type × block	2	0.013	10.91	0.007
Error	7	0.001		
June 1996				
Substrate type	2	0.0007	0.11	0.90
Block	1	0.003	0.41	0.53
Error	8	0.007		
August 1996				
Substrate type	2	0.41	11.09	0.005
Block	1	0.27	7.40	0.02
Error	8	0.037		

during day trials ($p = 0.0002$; Fig. 2*a*), while predation rates of yellow perch were similar during day and night ($p = 0.2267$; Fig. 2*b*). Bluegill predation rates were higher than those of yellow perch in the night trials.

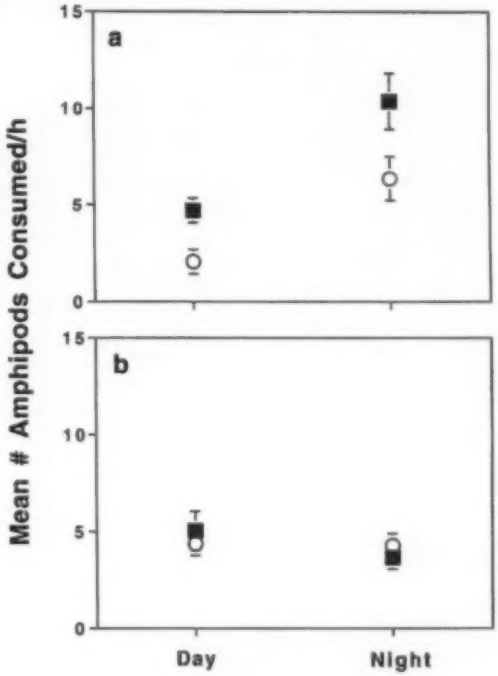
Discussion

Our results indicate that habitat complexity plays an important role in substrate preference of amphipods. When significant differences were detected, amphipods preferred substrates with mussel colonies over substrates with bare rock. Habitat preference by amphipods, however, varied seasonally. In both years, amphipods consistently preferred high-complexity substrates in late summer (August), while no significant preferences were observed earlier in the summer (June and July).

We observed significant differences in habitat preference during the spring experiment (May 1996). High variability between blocks, however, makes results more difficult to interpret. In this experiment, amphipod densities were greater in one block in the dead mussel treatment than in the other two treatments in one block. Water temperature during this experiment was also lower than in the other experiments. At this lower temperature the 7-day incubation period may have not been long enough for colonization rates to reach an asymptote as in the other experiments.

Recent studies have reported preference by amphipods for mussel colonies (dead and live) over bare rocks in the St. Lawrence River (Ricciardi et al. 1997) and Lake Erie (Stewart et al. 1998). Although the experimental design in these studies was similar to ours, their colonization times were considerable longer than in this study (68 and 37 days, respectively). This study is the only one to test for seasonal differences in amphipod habitat preference.

Fig. 2. Mean predation rates (±SE) of (*a*) bluegill and (*b*) yellow perch in aquaria with bare rocks (squares) and with zebra mussel colonies (circles). Error bars that are not apparent are smaller than the symbols.



We were not entirely successful in maintaining similar surface areas among treatments because it was difficult to estimate surface area in the live mussel treatment before the end of the incubation period. In 1995, surface area in the live mussel treatment was greater than in the bare rock (August) and dead mussel (July) treatments. Therefore, in 1996, we deliberately chose slightly smaller mussel colonies for the live mussel treatment than for the dead mussel treatment. Apparently, we overcompensated because in 1996, surface area was smaller in the live mussel colonies than in the other two treatments. Our measurement of habitat complexity, *S/V*, indicated a similar habitat complexity between dead and live mussels.

Food availability seems to play a weaker role than habitat complexity in amphipod habitat preference. Amphipods preferred live mussels over dead mussels in one experiment (August 1996). However, the importance of food availability in amphipod habitat preference may also vary seasonally. In addition, year-to-year variability in food resources may affect amphipod habitat preference. Similar to our results, Stewart et al. (1998) found no response by amphipods to differences in food availability between dead and live mussels in summer 1995, although organic matter deposition was greater in live than in dead colonies. In the western basin of Lake Erie, phytoplankton concentrations (mainly blue-green algae) were higher in late summer 1995 than in late summer 1996 (M.J.

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González, personal observation), which suggests that the amount of detritus reaching the bottom of the lake probably was higher in 1995 due to the higher overall settling rate of phytoplankton. Thus, preference for live mussels compared with dead mussels may depend on the relative availability of algae, detritus, and feces and pseudofeces and how well amphipods can use these food sources.

The seasonality in amphipod habitat preference in the lake may be linked to seasonal variability in predation risk. Several lines of evidence suggest that predation risk by fish may be greater in late summer than in early summer in Lake Erie and other habitats. First, total fish biomass increases during the summer (Hall and Werner 1977; Knight and Vondracek 1993; Roseman et al. 1996). Second, bioenergetics studies have shown an increase in fish feeding rates in late summer due to warmer temperatures (Kitchell et al. 1977; Luecke et al. 1990; Parrish and Margraf 1990). Third, although amphipods were the main dietary component of yellow perch in Lake St. Clair from April to August 1994, the maximum number of amphipods per stomach occurred in late summer (Synnestvedt 1997). Similarly, Thayer et al. (1997) reported an increase in the yellow perch electivity index for *Gammarus* sp. from June to October in pond experiments.

This study provides experimental evidence of the effect of zebra mussel presence on fish–amphipod interactions. Our laboratory experiments indicate that the spatial heterogeneity provided by mussel colonies can differentially alter predator–prey interactions. Bluegill consumption of amphipods significantly decreased in tanks with mussel colonies. In contrast, yellow perch consumption of amphipods was similar in the presence and absence of mussels. Ontogenic diet shifts have been documented for both fish species (Werner and Hall 1988; Wu and Culver 1992). Thus, the species-specific differences may be due to differences in food preferences of bluegill and yellow perch at the size used in the experiments. Several studies have documented a decline in the proportion of macroinvertebrates in the diet of bluegill larger than 80 mm compared with smaller fish. This shift in diet corresponds to a habitat shift from the littoral to pelagic areas (Mittelbach 1988; Werner and Hall 1988). On the other hand, yellow perch smaller than 30 mm are zooplanktivorous, while yellow perch larger than 50 mm consume mainly macroinvertebrates (Wu and Culver 1992; Roseman et al. 1996). Thus, the yellow perch used in our experiments may have been better adapted to capture amphipods than large bluegill, and therefore, yellow perch behavior may be less affected than bluegill behavior by zebra mussels. The refuge provided by zebra mussel colonies to amphipods may depend on mussel vulnerability to fish predation. Yellow perch are capable of preying on zebra mussels (Morrison et al. 1997). We observed fragments of mussel shells in the aquarium after the feeding trials with yellow perch, which may indicate its ability to attack and handle mussels. Thus, zebra mussel colonies may not be an effective refugium from yellow perch predation.

The differences in bluegill feeding rates during day and night experiments may suggest a differential vulnerability of amphipods to bluegill predation. Mundi (1959) documented a migration to the surface at night for *Hyalella azteca* in Lac la Ronge, England. Negative phototactic behavior has been documented for several amphipod species (Hunte and Myers 1984). If amphipods become more active during the night, they may be more vulnerable to bluegill predation.

In summary, our field experiments indicate that habitat complexity provided by zebra mussel colonies seems to be an important factor underlying the habitat preference of amphipods in Lake Erie. Furthermore, our laboratory experiments suggest that mediation of fish–amphipod interactions by zebra mussels depends on predator species identity. Thus the consequences of zebra mussel invasion on fish communities in Lake Erie may be complex and may depend on food web structure.

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A new approach to the analysis of stock–recruitment relationships: "model-free estimation" using fuzzy logic

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Abstract: In response to the need for overt recognition of uncertainty in management of natural resources, we present a new, innovative, causal approach for analysis of stock–recruitment relationships and prediction of recruitment. Applying principles and techniques developed from the theory of fuzzy sets, we demonstrate how heuristic reasoning can be used to define stock–recruitment relationships, explicitly characterise vagueness and uncertainty, and provide a functional relationship that combines stock size and past recruitment to predict future recruitment. The approach is termed model-free estimation or approximation. Tested on eight stock–recruitment data sets, there was no significant difference between recruitment predicted by the fuzzy approximation method and the Ricker or Beverton–Holt recruitment functions. We account for effects of nonstationarity by incorporating rules that relate past recruitment to future recruitment in the fuzzy stock–recruitment system. A weighting factor, w, represents the degree of belief in the importance of past recruitment and stock size in predicting future recruitment. The approach is robust with respect to the number of fuzzy sets used to define data clusters, can be tailored to individual circumstances, and thrives in data-poor situations where analytical methods may be inappropriate. It is a simple and broadly applicable solution with important implications for fish stock assessment and fisheries management in general.

Résumé : Conscients de la nécessité de reconnaître clairement l'incertitude existant dans la gestion des ressources naturelles, nous présentons une nouvelle approche causale novatrice pour l'analyse des relations entre stock et recrutement et pour la prévision du recrutement. En appliquant des principes et techniques découlant de la théorie des ensembles flous, nous démontrons comment le raisonnement heuristique peut être utilisé pour définir les relations entre stock et recrutement, pour caractériser explicitement le flou et l'incertitude et pour fournir une relation fonctionnelle qui combine la taille des stocks et le recrutement passé pour prévoir le recrutement futur. On donne à cette approche le nom d'estimation ou d'approximation sans modèle. Les essais sur huit ensembles de données stock–recrutement ont montré qu'il n'y avait pas de différence significative entre le recrutement prévu par cette méthode d'approximation et par les fonctions de recrutement de Ricker ou de Beverton–Holt. Nous avons tenu compte des effets de la non-stationnarité en incorporant des règles qui relient le recrutement passé au recrutement futur dans le système stock–recrutement flou. Un facteur de pondération, w, donne le degré de croyance en l'importance du recrutement passé et de la taille du stock pour la prévision du recrutement futur. L'approche est robuste quant au nombre d'ensembles flous utilisés pour définir les grappes de données, peut être adaptée aux circonstances et donne de bons résultats quand les données sont pauvres et que les méthodes analytiques peuvent être inappropriées. Il s'agit d'une solution simple et largement applicable qui peut s'avérer très utile dans l'évaluation des stocks de poisson et la gestion des pêches en général.

[Traduit par la Rédaction]

Introduction

Natural resource management demands recognition of the inherent variability of natural processes. In an attempt to satisfy these needs, analytical methods for explicit quantification of variability and uncertainty have pervaded the scientific discipline (Efron and Tibshinami 1991; Gelman et. al. 1995; Hilborn and Mangel 1997). Essential techniques in our methodological toolbox include likelihood methods, Bayesian analysis, bootstrapping, and multiple regression analysis, to name but a few. The root of many such techniques lies in having to create a model of how we think the world works.

Summarising complex data sets, we seek causal relationships to use in a variety of predictive analytical models. Within fisheries science, experience has shown that if a stock is fished hard, there is a point at which recruitment drops due to overfishing (Cushing 1971; Myers et al. 1995). Determining the relationship between stock and recruitment is the cornerstone for predicting how much parent stock can be reduced by fishing without negative impacts on future productivity. Environmentally related variation in recruitment also makes it one of the most difficult problems in the biological assessment of fisheries (Hilborn and Walters 1992). Based on biological assumptions of density-dependent regulation,

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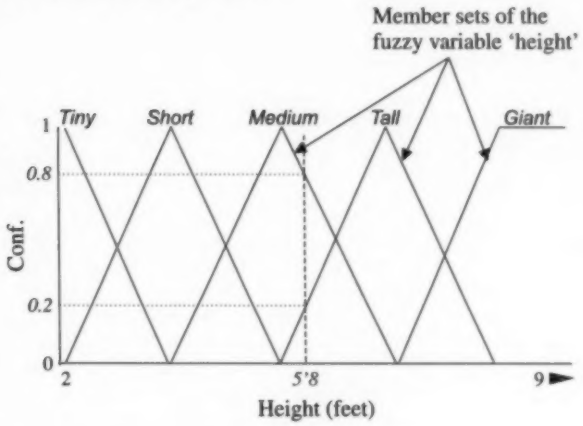
Fig. 1. Fuzzy sets on the fuzzy variable height. The sets (also sometimes called members or subsets) are the linguistic concepts *tiny*, *short*, *medium*, *tall*, and *giant*. The triangles are the membership functions of each set. The slope and degree of overlapping of the membership functions are the key element determining how unique or fuzzy each set is. The degree of confidence on the *Y*-axis shows our degree of belief in the linguistic concepts. For example, when Caroline's height is 5 ft 8 in., we are 0.8 confident that she is of *medium* height and also 0.2 confident that she is *tall*.



functional relationships are used to generate stock–recruitment curves with the dual intention of describing an average relationship between stock and recruitment and estimating recruitment for any given stock size. Such analyses form the building blocks of stock assessment and are thus a core element in fisheries science and management. Two well-known and widely applied analytical models are the Ricker and Beverton–Holt recruitment equations. Ricker's (1954) recruitment equation describes a group of humped curves that imply strong density dependence with low recruitment at high stock levels. Beverton and Holt's (1957) equation describes a group of asymptotic curves exhibiting constant recruitment beyond a certain stock density.

Fitting of these recruit curves is typically carried out by using an iterative least squares method, i.e., finding the best fit by minimising the residuals of all data points to a given curve. Uncertainty in the stock–recruitment relationship is typically calculated based on the likelihood of the observed data for different model parameterisations. Although more complex curves have been described that provide further generality from the assumptions concerning the form of the density-dependent compensation of recruitment (Paulik 1973; Deriso 1980; Garrod 1982; Shepherd 1982), typically, Ricker or Beverton–Holt type curves are used to describe stock–recruitment relationships, since they are believed to capture most of the needed behaviours (Hilborn and Walters 1992). However, dissatisfaction with the considerable deviations that often exist between parametric fits (such as the Ricker and Beverton–Holt relationships) to observed stock–recruitment data has prompted the application of nonparametric analysis (Rothschild and Mullen 1985) that can be used to analyse stock–recruitment data independent of assumptions on density-dependent mechanisms. A preliminary attempt that uses fuzzy control theory to estimate recruitment based on catch-at-age data was presented by Sakuramoto (1995).

We present a new approach for describing stock–recruitment relationships, characterising their vagueness, quantifying uncertainty, and providing a functional relationship that combines stock and past recruitment to predict future recruitment. It is a heuristic approach using methodological techniques developed on the principles of fuzzy set theory.

Fuzzy set theory in brief

Fuzzy logic was developed by Zadeh (1965). It is not a logic that is fuzzy, but a theory of fuzzy sets that is used to calibrate vagueness. It has a rigorous mathematical foundation that has been shown to encompass probability theory (Kosko 1990), rather than contradict it.

The essence of fuzzy logic rests on the truism that all things admit degrees of vagueness. Black and white cases are the exception in a world of gray. For example, the distinction between someone who is *medium* in height and someone who is *tall* is vague (Fig. 1). The categories overlap and may also shift in different contexts. The terms in italics are fuzzy terms. In set theory, each of these linguistic values is a set or member of the fuzzy variable height.

There is no one point where we can say someone is *tall* or *not tall*. It is a matter of degree. Similarly, natural systems do not conform to crisp definitions. Clearly, this is rather obvious, but conventional mathematical tools force break points. They insist on bivalence — yes or no, 0 or 1 — and thus forego the ability to deal with vagueness. We perceive the precise in a fuzzy way and it is this ability to summarise information into classes (fuzzy sets) that separates human intelligence from machine intelligence (Zadeh 1973). Using fuzzy set theory allows us to embrace and quantify the vagueness and uncertainty associated with data.

Fuzzy approximation theory

The techniques presented below adhere to the principles of fuzzy approximation theory (Kosko 1993*a*). Simply stated, this theory demonstrates that any curve can be approximated by covering it with patches. When data are sparse and uncertain, there are fewer and larger patches (Fig. 2*a*). Less fuzzy and increasingly rich data reduce the size and increase the number of patches (Fig. 2*b*). If the patches are so precise that they are not fuzzy, they then collapse to form points such that they approximate a curve.

An individual patch equates directly to a piece of knowledge, a single fuzzy rule of the form IF *this* THEN *that*. Rules make associations. They relate one thing or event or process to another thing or event or process (Kosko 1993*b*) and are the key to relating fuzzy sets. For example:

> IF shower water temperature *cool* THEN set temperature dial to *high*

where *cool* is a fuzzy set of shower water temperatures and *high* is a fuzzy set of temperature dial positions. Figuratively, we combine the base (support) of the two triangular membership functions, one for each fuzzy set (Fig. 3). The product of two line pieces provides a rectangle that defines

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Fig. 2. Fuzzy patches as approximators of curves. (*a*) Data poor with large uncertainty or fuzziness; (*b*) data rich with low uncertainty or fuzziness.

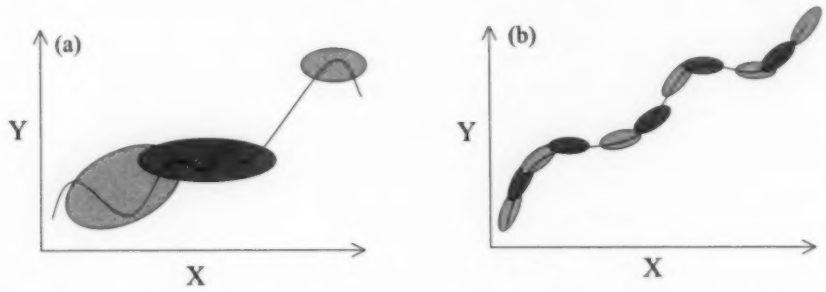
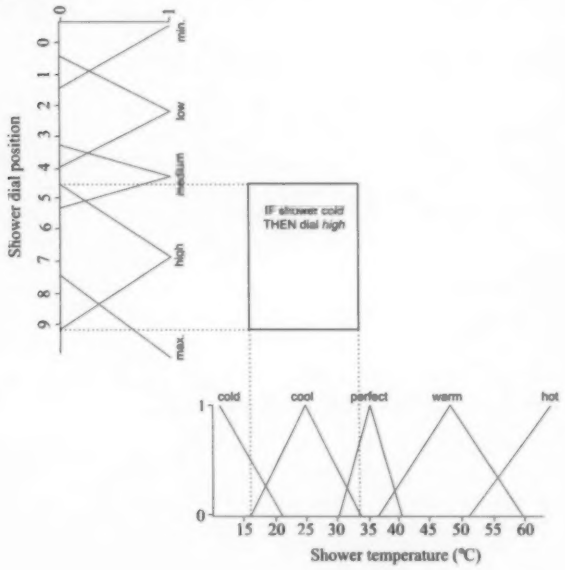


Fig. 3. Rules as patches. An important point is that the support (base width of the triangle) of fuzzy sets may vary in size. Small patches produce sets whose support is small (triangles with a narrow base) and large patches produce sets whose support is large (triangles with a wide base). The height of the triangles tells the degree to which a given value belongs to a patch.



the relationship of the fuzzy sets as a patch. Rule = patch and vice versa.

A bunch of patches (or rules) combine to produce a fuzzy system. In the example above, we would have a series of five rules or overlapping patches governing a system that controls the shower temperature by changes in the dial position. The fuzzy system lets you express what you know in a nonmathematical language. The technical term is model-free estimation or approximation (Kosko 1993*b*).

Stock–recruitment relationships are frequently riddled with patches that are not described well with analytical equations (e.g., see Myers et al. 1995). There is vagueness in the level of stock size and (or) recruitment and uncertainty in the relationship of the two. Employing the principles outlined above, it is possible to capture both of these aspects in a practical, quantitative, and intuitive way.

Model-free approach to stock–recruitment

We present below the model-free estimation approach that relates stock size and past recruitment to future recruitment. The approach incorporates three important principles of stock–recruitment relationships described by Hilborn and Walters (1992): (*i*) the average stock–recruitment relationship must pass through the origin, so that when there is no parental stock, there is no recruitment, (*ii*) continuity: the average stock–recruitment relationship does not change rapidly over a very small range of stock sizes, i.e., mean recruitment should vary smoothly with stock size, and (*iii*) stationarity: the average stock–recruitment relationship ought to be constant over time. However, there is substantial evidence that the concept of stationarity does not hold true. For many fisheries, there are multiyear and decadal fluctuations in recruitment that override large interannual variability, causing time-variant changes in the relationships between stock sizes and recruitment rates (Walters 1987; Bakun 1996). Serial correlation analysis of recruitment data for selected fish stocks showed that the most frequently occurring correlations were with a 1-year time lag (Hennemuth et al. 1980), i.e., recruitment rates ought to be similar in adjacent years due to the effects of either similar parental stock sizes or similar environmental conditions. In this paper, we therefore approach the nonstationarity of stock–recruitment relationships by combining with the effect of stock size, rules defining recruitment serial correlation based on the relationship between 1-year time lags in recruitment. These rules directly incorporate systematic changes of recruitment with time into the analysis of stock–recruitment.

The model-free approach to stock–recruitment consists of two stages: (1) using previous data to define the fuzzy system relating stock and past recruitment to future recruitment and (2) using the fuzzy system to predict recruitment. Embedded with stage 1 are two clustering techniques used to define the fuzzy sets on stock and recruitment. We offer a brief description of the situations under which each specific technique may be appropriate. We use the following abbreviations: stock size (SS), recruitment (R), recruitment last year (RLY). Figure 4 provides a diagrammatic overview.

Defining the fuzzy stock–recruitment system

Step 1

Plot data.

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Fig. 4. Diagrammatic overview of model-free estimation.

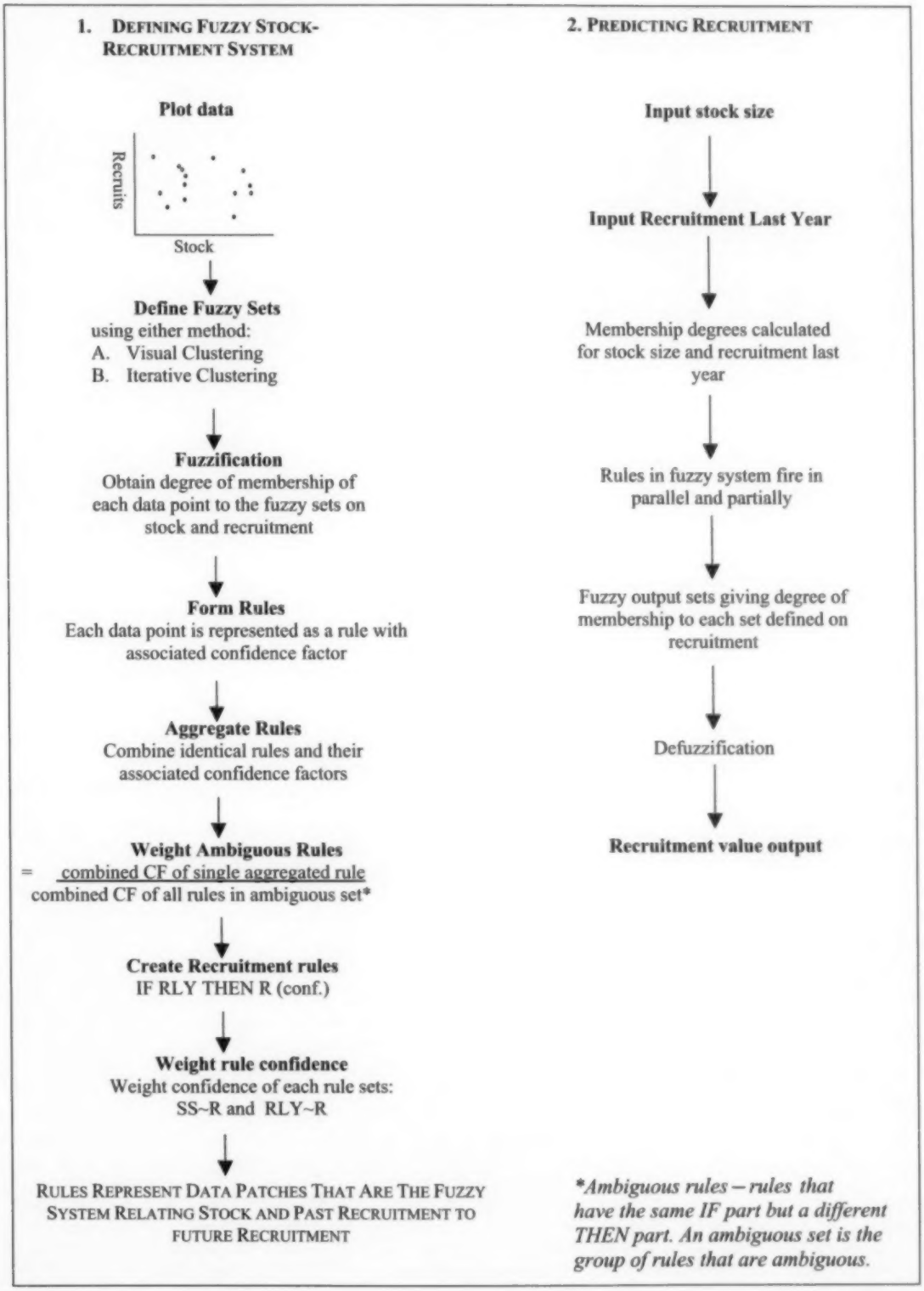
1. DEFINING FUZZY STOCK-RECRUITMENT SYSTEM
Plot data
Recruits
Stock
Define Fuzzy Sets
using either method:
A. Visual Clustering
B. Iterative Clustering
Fuzzification
Obtain degree of membership of each data point to the fuzzy sets on stock and recruitment
Form Rules
Each data point is represented as a rule with associated confidence factor
Aggregate Rules
Combine identical rules and their associated confidence factors
Weight Ambiguous Rules
= combined CF of single aggregated rule / combined CF of all rules in ambiguous set*
Create Recruitment rules
IF RLY THEN R (conf.)
Weight rule confidence
Weight confidence of each rule sets:
SS~R and RLY~R
RULES REPRESENT DATA PATCHES THAT ARE THE FUZZY SYSTEM RELATING STOCK AND PAST RECRUITMENT TO FUTURE RECRUITMENT
2. PREDICTING RECRUITMENT
Input stock size
Input Recruitment Last Year
Membership degrees calculated for stock size and recruitment last year
Rules in fuzzy system fire in parallel and partially
Fuzzy output sets giving degree of membership to each set defined on recruitment
Defuzzification
Recruitment value output
*Ambiguous rules – rules that have the same IF part but a different THEN part. An ambiguous set is the group of rules that are ambiguous.

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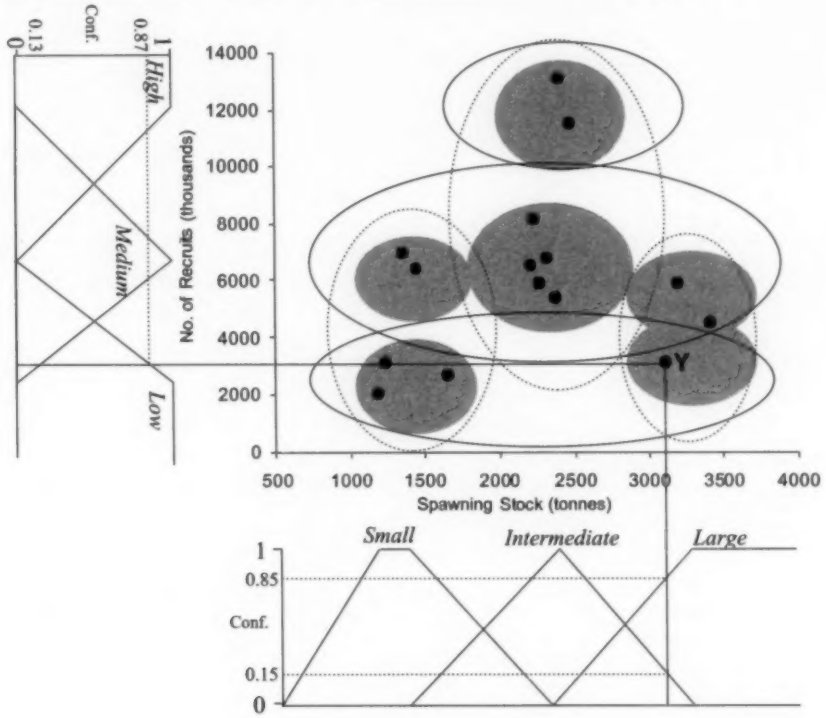
Fig. 5. Visual clustering on ICES Division VIIe plaice data. Supremum values are defined according to the centre of identified clusters in each plane. Dotted ellipses respresent approximate clusters on stock variable, and solid ellipses are approximate clusters on recruit variable. Shaded patches identify data clusters that equate to rules relating stock size to recruitment (see Table 2). Data point *Y* with value of SS = 3117 belongs to *intermediate* stock size to a degree of 0.15 and to *large* stock size to a degree of 0.85. Similarly the value *R* = 3062 belongs to *low* recruitment to a degree of 0.87 and *medium* recruitment to a degree of 0.13.



Step 2

Determine fuzzy sets on stock and recruitment axes (methods A and B outlined below).

Method A. Visual clustering: Method A is a visual approximation that relies on the ability to be able to define clusters or patches in the data. The technique has much in common with method B, iterative clustering, but may be more appropriate for use in the following circumstances: (*a*) when there is prior knowledge as to how data are clustered (i.e., if there is belief in causative relationships giving rise to the observed distribution of data), (*b*) when data are sparse and there is no access to a computer, (*c*) when there is large uncertainty associated with confidence in measurements of stock size or recruitment, and (*d*) applied as a rough and ready approximation when there is no evident pattern in the data and it is necessary to impose sets by simply discretizing the data into intervals. The procedure is as follows.

(*i*) The data are visually inspected and approximate patches or clusters in the vertical and horizontal planes are defined (i.e., on stock size and recruitment). If prior knowledge of a relationship between stock and recruitment exists, then this information is used to help define clusters.

(*ii*) From the centre of each cluster, a line is drawn to each axis. This is the supremum value and represents the peak of each fuzzy set (Fig. 5). For the middle sets, we draw triangular membership functions on each axis. The base of each triangle (support of the fuzzy sets) is extended to the supremum of adjoining sets. Drawn like this, the sets have a high fuzziness, which is an expression of our uncertainty in the data. Furthermore, it ensures that the system adheres to the principle of continuity. Trapezoid shape membership functions are drawn for inner and outmost sets. For the set of *small* stock size, the trapezoid is drawn such that after the lowest value of stock size, the membership declines to the origin. This fulfils the necessity of having zero recruits when stock size is zero but also assumes that below the lowest observed value of stock size, recruitment declines gradually to zero. Note that the membership functions do not necessarily have the same base width.

(*iii*) Each set is given a label, e.g., *small*, *medium*, *large*.

Method B. Iterative clustering: In contrast with the visual clustering method, iterative clustering defines patches or clusters according to an iterative scheme that minimises an objective function. The core element relies on an impartial fuzzy cluster analysis routine (Bezdek 1981) from which fuzzy sets are defined (Appendix). We propose that this technique is most suited when (*a*) there is an abundance of data, (*b*) there is no prior knowledge as to causative relationships,

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Table 1. Fuzzification of data instances for ICES Division VIIe plaice (1976–1990).

		Membership degrees								
		Stock size			Recruitment			Rule		
Stock	Recruits	*Small*	*Intermediate*	*Large*	*Low*	*Medium*	*High*	IF part	THEN part	CF
1188	2 005	1			1			*Small*	*Low*	1
1235	3 081	1			0.86	0.14		*Small*	*Low*	0.86
1358	6 966	1				0.96	0.04	*Small*	*Medium*	0.96
1443	6 395	0.96	0.04		0.08	0.92		*Small*	*Medium*	0.87
1658	2 641	0.73	0.27		0.97	0.03		*Small*	*Low*	0.70
2272	5 885	0.08	0.92		0.20	0.80		*Intermediate*	*Medium*	0.73
2383	5 378		0.96	0.04	0.32	0.68		*Intermediate*	*Medium*	0.65
2323	6 780	0.03	0.97			0.99	0.01	*Intermediate*	*Medium*	0.97
2208	6 490	0.15	0.85		0.06	0.94		*Intermediate*	*Medium*	0.80
2405	13 117		0.94	0.06			1.00	*Intermediate*	*High*	0.94
2470	11 521		0.87	0.13		0.17	0.83	*Intermediate*	*High*	0.72
2235	8 166	0.12	0.88			0.75	0.25	*Intermediate*	*Medium*	0.66
3117	3 062		0.15	0.85	0.87	0.13		*Large*	*Low*	0.74
3419	4 474			1	0.54	0.46		*Large*	*Low*	0.54
3201	5 883		0.05	0.95	0.20	0.80		*Large*	*Medium*	0.75

(*c*) there are computing facilities, and (*d*) there is uncertainty about the validity of data. The procedure is as follows.

(*i*) Data clusters are determined automatically by a cluster routine (Appendix). Briefly, the routine defines the optimum number of patches to describe the data and provides the cluster centroid position (supremum), support of the membership functions, and degree of membership of each point to any cluster. By modification of the algorithm given by Bezdek (1981), we are able to define asymmetric membership functions. This element is central in providing a description of the data with the minimum possible number of sets. As previously described, triangular membership functions are used for the middle sets and trapezoids at the edges.

(*ii*) Each set is given a label, e.g., *small*, *medium*, *large*.

Step 3

All the data are "fuzzified". Each point is expressed using the label and confidence value from the fuzzy set or sets within which it falls. For example, consider data point *Y* in Fig. 5. The value of SS = 3117 belongs to *intermediate* stock size to a degree of 0.15 and to *large* stock size to a degree of 0.85. Similarly the value R = 3062 belongs to *low* recruitment to a degree of 0.87 and *medium* recruitment to a degree of 0.13.

Step 4

Each stock–recruitment data instance is now represented by one fuzzy rule by taking the fuzzy labels to which a data point belongs to the highest degree. In the above example, data point *Y* is expressed as the rule IF SS *large* THEN R *low*. A confidence factor (CF) for each of the rules is calculated by multiplying the membership degree of each of the elements (the IF part and the THEN part); in the above example, CF *large* × CF *low* = 0.85 × 0.87 = 0.74. Table 1 follows a complete example of how rules are formed for each data instance.

Step 5

The next step defines a single set of rules by aggregating the rules obtained in step 4. Using an example from the values in Table 1, we demonstrate how we arrive at the values in Table 2. Firstly, stock–recruitment data instances whose IF and THEN parts are identical are now aggregated. The CF associated with each data instance is summed to form one single rule with a combined total CF. From Table 1, two data instances provide the same rule: IF SS *small* THEN R *medium*. The sum of their individual confidences is 0.96 + 0.87 = 1.84 (Table 2). There are now six rules that relate stock size to recruitment. Note that some of these are ambiguous (rules in which the IF parts are the same but the THEN parts are different). In our example, the rules IF SS *small* THEN R *low* and IF SS *small* THEN R *medium* are said to form an ambiguous set.

Secondly, the CF for each rule is calculated using a normalised weighting method that adjusts the CF based on the combined sum of CF of the ambiguous set. For each rule, we take the sum of individual rule CF's for that rule and divide it by the combined sum of CF of all the rules that belong in the ambiguous set. Returning to our example, the "ambiguous weighted CF" is calculated as

IF SS *small* THEN R *low* 2.57/4.40 = 0.58

IF SS *small* THEN R *medium* 1.84/4.40 = 0.42.

The weighting method leaves both rules intact but weights the CF's according to their frequency and combined CF's from individual data instances. The set of extracted rules define the relationship between stock and recruitment (Table 2).

Step 6

A set of rules is created that relates recruitment last year (RLY) to 1 year hence (R). These rules are derived by simply combining the fuzzy labels and CF's of recruitment last year with recruitment, forming rules of the form IF RLY THEN R, as shown below. The obtained fuzzy rules are ag-

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Table 2. Set of extracted fuzzy rules (with associated CF) that comprise the fuzzy system.

Combined rules	Sum of individual rule CF's	Combined ambiguous CF	Ambiguous weighted rule CF	Final rule CF (w = 0.8)
SS–R rules				
IF *small* THEN *low*	2.57		0.58	0.47
IF *small* THEN *medium*	1.84	4.40	0.42	0.33
IF *intermediate* THEN *medium*	3.81		0.70	0.56
IF *intermediate* THEN *high*	1.66	5.47	0.30	0.24
IF *large* THEN *medium*	0.75		0.37	0.3
IF *large* THEN *low*	1.28	2.03	0.63	0.5
RLY–R rules				
IF *medium* THEN *medium*	3.60		0.62	0.12
IF *medium* THEN *low*	1.44		0.25	0.05
IF *medium* THEN *high*	0.80	5.85	0.14	0.03
IF *low* THEN *medium*	2.61		0.59	0.12
IF *low* THEN *low*	1.85	4.47	0.41	0.08
IF *high* THEN *medium*	0.76	0.76	1	0.2
IF *high* THEN *high*	0.81	0.81	1	0.2

Note: Weight factor (w), which represents the degree of belief in importance of stock size and past recruitment in determining future recruitment, was set at 0.8. Data for ICES Division VIIe plaice (1976–1990).

gregated to define a set of rules each with a CF as outlined in step 5 (Table 2).

Time	IF	RLY	THEN	R
1		*High*	→	*High* (CF)
2		*High*	→	*Low* (CF)
3		*Low*	→	*Low* (CF)
4		*Low*		

Step 7

The rules sets are weighted. There are now two sets of rules, one relating stock to recruitment and another relating past to future recruitment. The confidence associated with each rule is multiplied by a weight ($0 > w > 1$) that represents our degree of belief in how important stock size and past recruitment are in determining future recruitment (Table 2). The combined weighted sets of rules is the fuzzy system. It predicts recruitment as the combination of two parts.

To facilitate the drawing of fuzzy set membership functions and performing fuzzy inference and centroid defuzzification, software specifically created for the development of fuzzy systems was used. Many such software tools are available on the web. Some freeware tools include FuzzyCOPE (http://divcom.otago.ac.nz:800/com/infosci/kel/fuzzycop.htm), FuzzyCLIPS (http://ai.iit.nrc.ca/fuzzy/fuzzy.html), and JFS (http://inet.uni2.dk/~jemor/jfs.htm). Two commercial tools are ReSolver (http://multilogic.com/software/software.cfm) and RAMAS RiskCalc (http://www.ramas.com/riskcalc.htm).

Predicting recruitment

To predict recruitment given new data instances of stock size and recruitment last year, a product fuzzy inference is used on the set of extracted rules. It is based on a multiplication between the degree of membership to the fuzzy sets on stock size and recruitment last year (IF parts) to which a new instance belongs and the centroid defuzzification method. Simply put, this is a weighted average value of recruitment calculated by multiplying the supremum value of each fuzzy set on recruitment by its respective degree of membership.

Let us follow a complete example. Consider the 1982 stock size of 2383 for ICES Division VIIe plaice. Recruits in the previous year were 5885. What are the predicted recruits?

Step 1

Using membership functions defined in Fig. 5, we determine that SS = 2383 belongs to sets *intermediate* to a degree of 0.96 and *large* to a degree of 0.04. Similarly, RLY = 5885 belongs to recruitment sets *low* (0.2) and *medium* (0.80).

Step 2

In the fuzzy system, these data are compared with the known rules (Table 2). The system has four rules relating to stock size *intermediate* and *large* and another five rules relating to recruitment last year *low* and *medium*. Consistent with Table 2, we take the value of w = 0.8, and thus, each rule has an associated CF, so all nine fire partially and in parallel, since all are true to a degree.

Given the degrees of membership to each set associated with stock size and recruitment last year, the rules fired are as follows.

SS–R rules

(1) IF SS *intermediate* (0.96) THEN R *medium* (CF = 0.56)

(2) IF SS *intermediate* (0.96) THEN R *high* (CF = 0.24)

(3) IF SS *large* (0.04) THEN R *low* (CF = 0.50)

(4) IF SS *large* (0.04) THEN R *medium* (CF = 0.30).

RLY–R rules

(5) IF RLY *low* (0.2) THEN R *medium* (CF = 0.12)

(6) IF RLY *low* (0.2) THEN R *low* (CF = 0.08)

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(7) IF RLY *medium* (0.8) THEN R *medium* (CF = 0.12)

(8) IF RLY *medium* (0.8) THEN R *low* (CF = 0.05)

(9) IF RLY *medium* (0.8) THEN R *high* (CF = 0.03).

Step 3

The combined confidences (CC's) of fuzzy output are calculated. Note that rules 1, 4, 5, and 7 conclude that recruitment is *medium*. When consequences (THEN parts) are the same as in this case, the CC for each term is calculated in a series as (Exsys Incorporated 1997)

$$\text{CC} = \text{current CC} + [(\text{value CF} \times \text{rule CF}) \times (1 - \text{current} \times \text{CC})].$$

Starting with rule 1, the current CC is zero; we have

$$\text{CC} = 0 + [(0.96 \times 0.56)(1 - 0)] = 0.54.$$

Now, combining the CF from rule 4:

$$\text{CC} = 0.54 + [(0.04 \times 0.30)(1 - 0.54)] = 0.55$$

and combining the CF from rule 5:

$$\text{CC} = 0.55 + [(0.2 \times 0.12)(1 - 0.55)] = 0.56$$

and combining the CF from rule 7:

$$\text{CC} = 0.56 + [(0.8 \times 12)(1 - 0.56)] = 0.60.$$

We have 0.60 confidence that recruitment is *medium*. The confidences in recruitment *low* and *high* are calculated in the same way. So, for SS = 2383 and RLY = 5885, we have the fuzzy output that recruits are *low* (CF = 0.05), *medium* (CF = 0.60), and *high* (CF = 0.25).

Step 4

To get a single value for recruits, we have to replace the set with a number. This is called defuzzification. We use the centre of mass or centroid of the output fuzzy sets. In practice, this is simply the supremum value of each membership function on the fuzzy variable recruitment weighted by the CF associated with each output set. In this example, predicted recruitment is therefore

$$\text{R} = (0.05 \times 2500) + (0.60 \times 6750) + (0.25 \times 12\,500) = 7312.$$

It is noteworthy that by performing the same method of defuzzification over the minimum and maximum values of each fuzzy set defined for the output variable, i.e., recruitment, it is possible to obtain a range around the single output value. This is a pragmatic way of providing a pseudo-output distribution, but is highly dependent on the base width of the fuzzy sets defined for the output variables. Details of the method are described in Mackinson and Newlands (1998).

Results from application of approach

By assigning a weight value, $w = 1$, the approach detailed above was applied to describe the relationship between stock and recruitment on data taken from Myers et. al. (1995). Both cluster techniques were applied to each data set (Fig. 6).

It is clear from the results demonstrated in Fig. 6 that the model-free estimation approach is capable of describing stock–recruitment relationships. A comparison of residuals between recruitment values predicted by Ricker or Beverton–Holt curves and the fuzzy approximations revealed no significant difference (t test on combined data, with unequal variance, $t = 0.06$, $P = 0.96$). However, Ricker or Beverton–Holt curves had fractionally lower sums of residuals in five of the eight data sets analysed. There was also no significant difference in the recruits predicted by the alternative cluster methods. As is evident from Fig. 6, they were in most cases very similar despite differences in the number of sets used on each axis (Table 3). This demonstrates the robustness of the techniques. The maximum number of sets required to capture the pattern in data on any one of the axes was four. In the majority of cases, three sets were sufficient.

Running the fuzzy system with $w < 1$ ensures that rules relating recruitment last year to future recruitment are fired in parallel with those that relate stock to recruitment. The implication is that we have dispensed with the assumption of stationarity, since predicted recruitment is dependent not only on stock size but also on recent history of recruitment. Reducing w results in a divergence from a smooth curve as the assumption of nonstationarity becomes increasingly important (Fig. 7). Note that continuity of the relationship between stock size and recruitment is not broken; rather, it becomes blurred when the two effects are combined on a plot of stock against recruitment. Two responses encountered when combining the effects of stock size and past recruitment are presented (Fig. 7). In the case of Pacific halibut (Figs. 7*a*–7*d*), lower weights on the importance of stock size increase the ability of the fuzzy system to track the observed changes in recruitment (i.e., reduce the sum of residuals), which implies that recent recruitment data provide better information to recruitment prediction than parental stock size. The contrary is true for Skeena River sockeye salmon (Figs. 7*e*–7*h*), where parental stock size has a higher influence on the observed recruitment pattern. In other cases, a plot of the sum of residuals was dome shaped, indicating more than one weight factor at which equally good fits were found. This emphasises the uncertainty of the role of stock size and systematic environmental changes in the observed recruitment variation.

Discussion

One of the tasks of stock assessment is to establish degrees of belief in different states of nature or hypotheses about biological processes of importance to decision making. Typically, this involves putting weights or probabilities on different parameter combinations of a model used to describe the relationship between two variables. The model-free approach offers a new and alternative way of expressing uncertainties in the relationship between variables by means of vagueness in the definition of the variables, the shape of the membership functions, and the actual clustering and overlap of the data among the different fuzzy sets. Uncertainties are then expressed in terms of fuzziness rather than probabilities. Although both describe uncertainty numerically, probability treats yes/no occurrences and is inherently statistical. Fuzziness deals with degrees and is completely nonstatistical (Zadeh 1965). A fuzzy system lets us guess at the nonlinear

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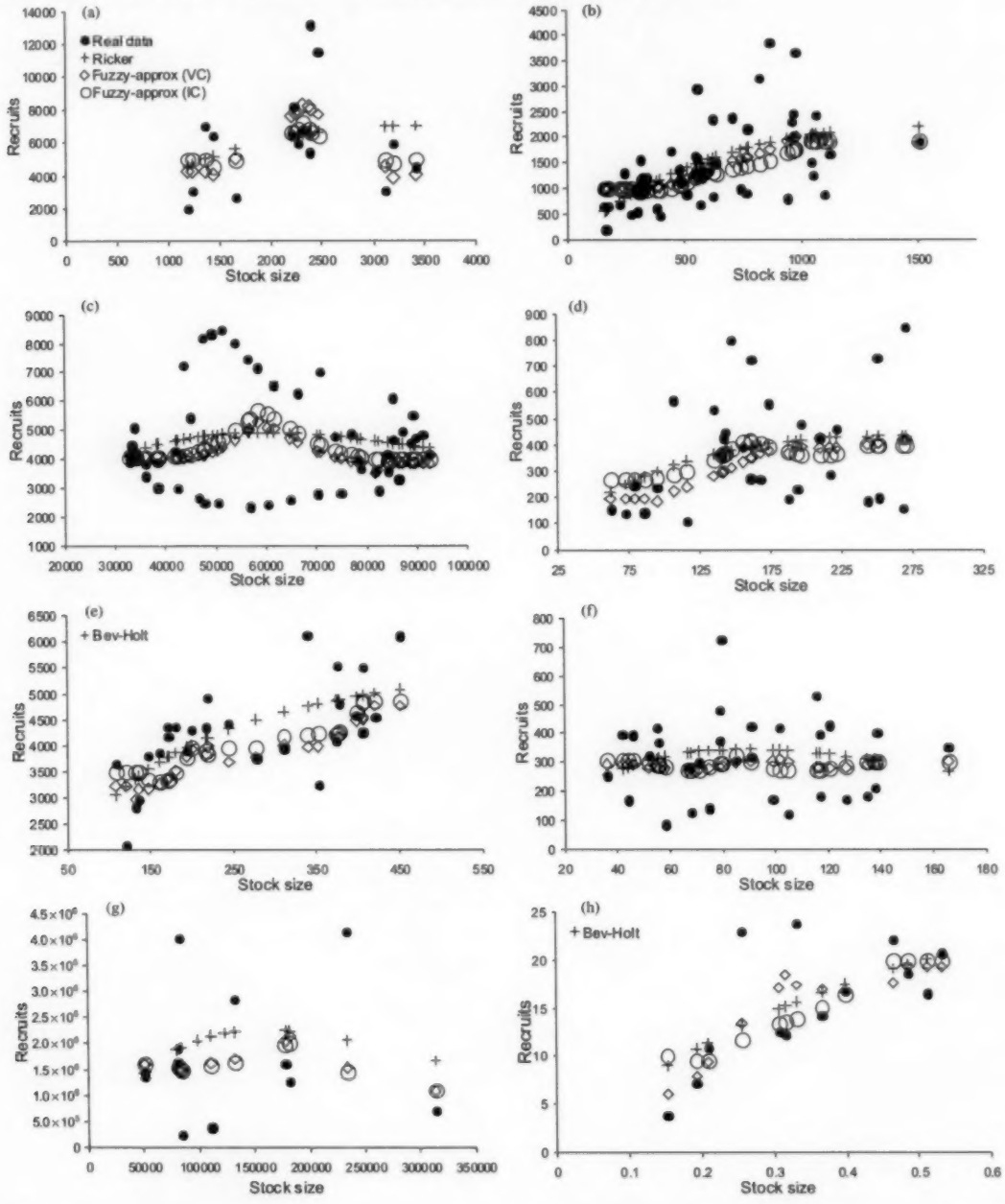
Fig. 6. Stock–recruitment data with comparison of the fuzzy approximation approach and traditional analytical methods. With the exception of Brasilian sardine, all data are taken from Myers et al. (1995). (*a*) ICES Division VIIe plaice; (*b*) Skeena River sockeye salmon, (*c*) Canadian and American Pacific halibut; (*d*) North Sea Atlantic cod; (*e*) southern bluefin tuna; (*f*) northern British Columbia chum salmon; (*g*) NAFO 4WX Atlantic herring; (*h*) Brasilian sardine (Cergole 1995).



world and yet does not make us write down a mathematical model of it (Kosko 1993*b*).

Since recruitment subsumes many natural processes that vary between years and species, it is reasonable to expect that most stock–recruitment relationships will display a large degree of scatter (Pitcher and Hart 1990). Moreover, if stock or recruitment has not been measured accurately, a discernible relationship may not be apparent or otherwise simply because one does not exist (Hilborn and Walters 1992). Traditional stock assessment science forces us to learn about nature by contrasting competing ideas or hypotheses against observations, and by fitting a stock–recruitment function, we place the data under an assertion of belief in density dependence. Given the current evidence on stock–recruitment rela-

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Table 3. Comparison of number of sets used in visual (VC) and iterative cluster (IC) methods.

	Number of sets			
	Stock		Recruits	
	VC	IC	VC	IC
Plaice (*Pleuronectes platessa*)	3	3	3	2
Sockeye salmon (*Oncorhynchus nerka*)	4	3	3	2
Pacific halibut (*Hippoglossus stenolepis*)	3	3	2	2
Atlantic cod (*Gadus morhua*)	3	3	3	2
Bluefin tuna (*Thunnus thynnus*)	4	4	3	3
Chum salmon (*Oncorhynchus keta*)	3	3	2	2
Atlantic herring (*Clupea harengus*)	3	3	2	2
Brasilian sardine (*Sardinella brasiliensis*)	3	3	3	2

tionships (see Myers et al. 1995), there are instances in which continuous functions are not well suited for describing the data, the result being that we fit curves that do not fit our beliefs. In contrast with this, the model-free approach approximates the relationship between stock and past recruitment to future recruitment with a set of heuristic rules free of the necessity of such a prior assumption. Since the essence of the approach relies upon "letting the data tell you", it has the ability to generate hypotheses rather than imposing them and thus provides tailor-made stock–recruitment relationships.

Application shows that in comparison with the analytical functions of Ricker and Beverton–Holt, fuzzy approximations of stock–recruitment relationships (with $w = 1$) fit the observed data at least as well, are robust with respect to the number of sets required to describe the data, and capture some important behaviours of the relationship. The major benefit is that there is no need to form hypotheses or build a model and determine its parameters prior to fitting the approximation.

Many marine fish populations show systematic long-term changes in recruitment success, which makes predictions based on uncorrelated, white noise recruitment variability degrade rapidly (Steele 1996). By combining rules in a fuzzy system and introducing a simple weight factor ($0 < w < 1$) that represents our belief in the importance of stock size and past recruitment in predicting future recruitment, nonstationary effects are explicitly incorporated into the analysis of stock–recruitment. Sensitivity analysis is provided by an examination of how closely predicted recruitment fits observed recruitment for all values of w. Stock weight (w), however, ought to vary depending on the range of observed stock sizes and thus on the history of the fishery. For instance, severely depleted stocks are expected to show reductions in recruitment as a result of overfishing that may cause w to be close to 1 (see Skeena River sockeye salmon, Fig. 7). Although a plot of residuals tells us what value of w provides the best fit of predicted to observed recruitment, we should not infer from this that it is the correct fit. It contains no information other than suggesting alternatives. Residual plots for Atlantic herring, Brasilian sardine, Atlantic cod, and chum salmon were dome shaped providing two values of w that gave equally good fits. Prior knowledge could be used for guidance and arbitration over which values of w to focus our intention on.

The choice for the value of w represents, in a sense, one the most fundamental debates in fisheries, i.e., about the relative importance of environmental factors and factors related to stock size in leading to fisheries collapse and policy failures. Among the most documented examples are the sardine/anchovy collapses in coastal upwelling systems (Lluch-Belda et al. 1989), the decline in recruitment of groundfish stocks off the east coast of North America (Walters and Maguire 1996), and the "Thompson–Burkenroad" debate on the causes of recruitment fluctuations in the stock of Pacific halibut (Parma and Deriso 1990). In the analysis of Pacific halibut data (Fig. 7) the fact that recruitment variation is better explained by past recruitment suggests a higher degree of beleif in an external forcing that causes recruitment to be similar in adjacent years. That does not imply, however, that we should rely on a single value of w as a best descriptor of the dynamics of a particular stock, but rather that all possible values should be weighted by data and by our prior knowledge to make uncertainty explicit in the analysis and prediction of recruitment. In this context, we see the model-free estimation approach as a comprehensive framework where the risks of candidate harvest policies can be analysed based on the uncertainties in the stock–recruitment relationships.

Hilborn and Walters (1992) briefly described two methods that resemble techniques presented here. The first, termed rough and ready, classifies data into subjective intervals to provide mangers with approximate guidelines. They provided the example "Stocks between 0 and 150,000 tons normally produce recruitments between 30 and 200 with occasional production as high as 600. Spawning stocks over 200,000 tons produce average recruitments of approximately 500 with an occasional very high production". The second method is simply a more formal method of the rough and ready approach. Tabular or Markov models also discretise the data into intervals. They calculate the probability of any spawning stock interval producing a recruitment in any of the possible recruitment intervals. This technique demands much data and suffers from having to assign explicit probabilities to describe all possible events. Getz and Swartzman (1981) and Overholtz et al. (1986) have used the method. In comparison with the techniques based on fuzzy logic, these methods go only part way in the analysis of stock–recruitment. In addition, the model-free estimation approach does not suffer when data are limited or of questionable validity. The result is that there are fewer sets, but they overlap more. Conclusions can still be drawn.

The two techniques used to define the clusters differ in complexity and in the context in which each is appropriate. Providing these alternative techniques can be likened to having several models to describe data. It allows the user to chose that approach that is best suited given the richness and validity of the data. An additional technique that we have not explored in this paper is the derivation of rules by using a neural network. A neural network senses fuzzy patterns in

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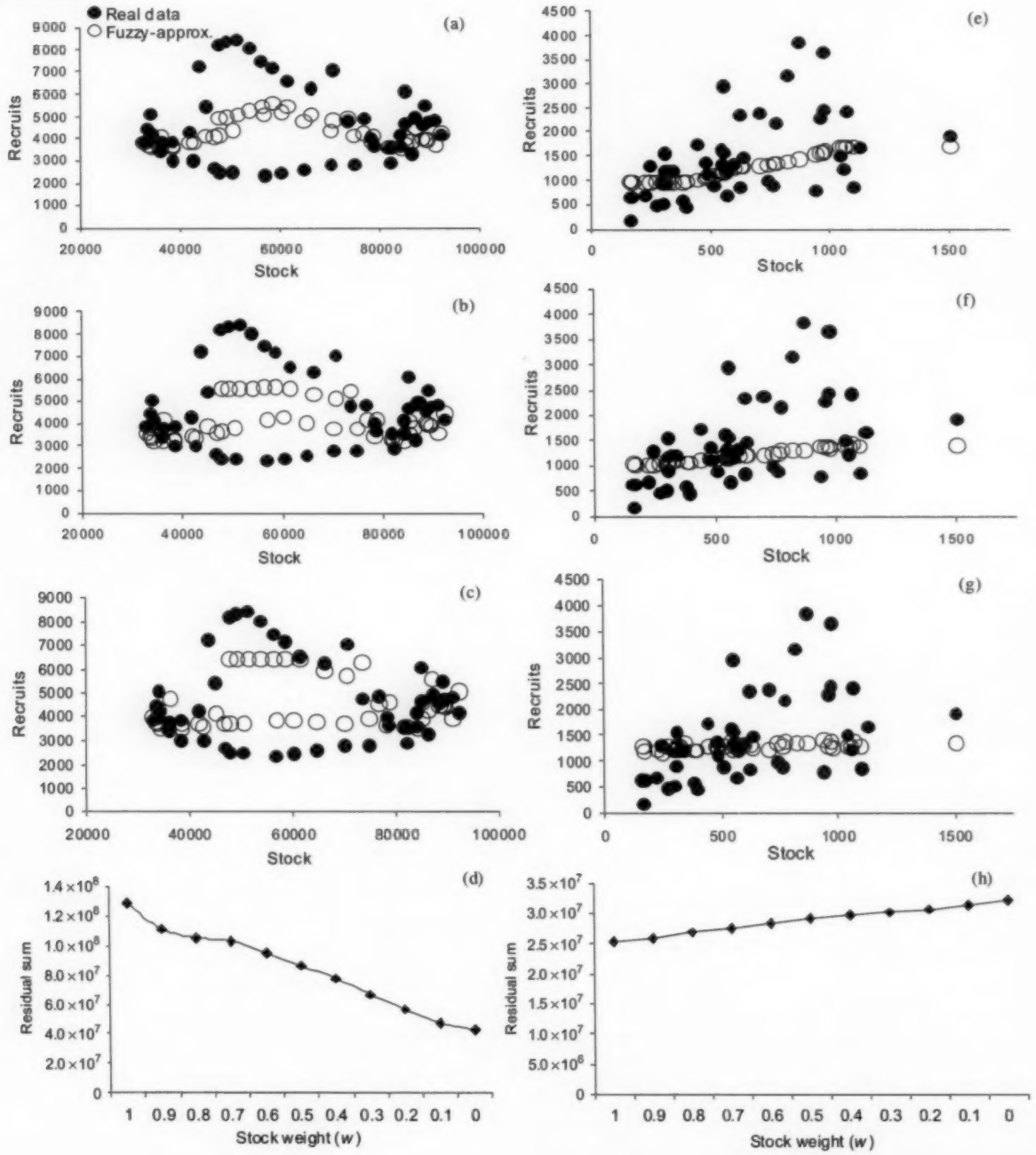
Fig. 7. Combined effects of stock size and past recruitment on predicted recruitment for two species. Pacific halibut: (*a*) $w = 0.8$, (*b*) $w = 0.4$, (*c*) $w = 0.1$, and (*d*) sum of residuals; Skeena River sockeye salmon: (*e*) $w = 0.8$, (*f*) $w = 0.4$, (*g*) $w = 0.1$, and (*h*) sum of residuals.



data and learns to associate the patterns. The patterns are rules. Kosko (1993*b*) and Kasabov (1996) provided detailed accounts of the principles of techniques for developing these adaptive fuzzy systems. Saila (1996) specifically addressed the potential use of neural networks in fisheries science.

Ecosystem processes, fish population dynamics, and natural processes in general do not yield well to description by conventional analytical techniques. Their complexity, nonstationarity, nonlinear, even chaotic features defy conformity. In defence, our suite of analytical tools has expanded to embrace the associated uncertainty and error. Hilborn and Mangel (1997) commented that "although the output of most

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models is numerical, the most influential models are the ones in which the numerical output is not needed to guide the qualitative understanding". Assigning labels to describe fuzzy sets provides a means to produce a qualitative output. Relationships can be easily explained and understood by their natural language heuristic rules that define them. In comparison with an equation, it is easy to compare such rules with the knowledge on specific biological and ecological characteristics, and in doing so offers a powerful tool to combine both scientific and nonscientific knowledge (Mackinson and Nøttestad 1998). Model-free estimation of stock–recruitment relationships fulfils the criteria that Hilborn and Mangel (1997) defined for useful models: "a model is most effective if it provides both understanding (of known patterns) and prediction (about situations not yet encountered)". Several other specific characteristics of the approach offer it as an attractive alternative for use in stock assessment in general.

(1) Characterises data richness and complexity and thrives in data-poor situations, since the approximation is looking for patches, not a linear relationship.

(2) It is adaptive. More data generate more clusters and rules; thus the approximations become better with more data.

(3) Few fuzzy sets are required to describe the data (two to four is clearly reasonable) to produce good approximations. Shapes of fuzzy set membership functions can be drawn as bell curves, trapezoids, or anything else, but in practice, triangles work fine. It is a matter of common sense and judgement (Kosko 1993*b*).

(4) By-hand analysis is possible, since data patches can be identified visually.

Use of heuristics combined with theory of fuzzy sets provides intuitive and practical methods that are being widely adopted across many disciplines. In the field of process control, engineers have clearly demonstrated that a system of rules is easier to derive and faster to use. Looking toward future applications in natural resource management, and fisheries in particular, we briefly identify possible areas of application.

(*i*) Descriptive and predictive modelling. Models of natural processes could benefit tremendously from use of fuzzy concepts. The use of fuzzy algorithms allows development of systems not bound by linearity, continuity, or stationarity. Despite incomplete, uncertain, and qualitative information, the system can be defined in terms of rules describing processes. In so doing, we also identify areas in which knowledge (rules) is lacking, thus focussing on potential research areas. Such models can be used to demonstrate how the behaviour of complex systems changes. One such model currently under development is the prediction of structure and distribution of herring shoals (S. Mackinson, in preparation). The system incorporates knowledge on biological and environmental factors determining the behaviour of herring. Another current project uses fuzzy logic in a spatial analysis of schooling dynamics and migration of tuna (N. Newlands, personal communication).

(*ii*) Risk assessment and decision analysis. An important aspect of decision making involves the explicit consideration of uncertainties and risks when evaluating possible management actions. Decisions on environmental issues are usually complex involving many components and variables with little quantifiable processes. Fuzzy heuristic systems provide an alternative approach to the description of uncertainties in situations too complex or too ill defined to allow precise mathematical analysis, offering a simple framework to gather information and to combine expert and lay-expert knowledge by means of linguistic variables and rules. Alternatively, it is possible to use the heuristic approach to better define the limits and distribution of the prior probabilities for Bayesian decision analysis.

(*iii*) Pattern recognition in data structures. The method of iterative clustering in model-free estimation of stock–recruitment relationships provides a good example. We identify and generate patches using a fuzzy cluster algorithm and then associate stock and recruitment by defining rules in a fuzzy system. Looking for patterns in spatial data is another obvious source of this type of application. For large data structures, neural networks can be used to search for patterns.

(*iv*) Incorporating local/traditional ecological knowledge with scientific knowledge for use in assessment and management. Most people use simple rules to make decisions and describe processes. The rule themselves are often vague. These heuristics are the food of fuzzy sets and the key to incorporating local knowledge in a formal scientific manner (Mackinson and Nøttestad 1999).

(*v*) Acoustic data filtering for identification of fish species and schools. Using fuzzy sets, simple rules could be implemented to describe conditions for selecting schools of fish from acoustic outputs. Selection criteria may include rules on echo intensity and number of continuous pings within a signal.

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Appendix. Fuzzy cluster analysis

The fuzzy *c*-means (FCM) clustering algorithm (Dunn 1974; Bezdek et al. 1987) partitions the stock–recruitment data, $X,Y = \{x_k, y_k ; k = 1, 2,..., n\}$, into i partitions, $1 \le i \le c$ ($c > 2$), which optimise a weighted sum of squares error of the objective function, J_m. A nondegenerate Fuzzy *c*-partition of X (or Y) is represented by the matrix $U = [\mu_{ik}] \in R^{cn}$.

$$\text{(A1)} \quad J_m(U, d) = \sum_{k=1}^{n} \sum_{i=1}^{c} (\mu_{ik})^m (d_{ik})^2$$

where m is the fuzziness index ($1 < m < \infty$) and $m = 2$ is used in this stock–recruitment analysis. The objective function, J_m, is used in determining a separation validity function, S (Xie and Beni 1991), which measures the overall average compactness and separation of the fuzzy *c*-partitions:

$$\text{(A2)} \quad S = \frac{J_2}{n \cdot (d_{\min})^2}$$

where $J_2 = J_m$ ($m = 2$), and $(d_{\min})^2$, termed the separation of the fuzzy *c*-partition, is calculated from $d_{\min}$ being the minimum distance between cluster centroids:

$$\text{(A3)} \quad d_{\min} = \min_{i,j} \left\| \mathbf{v}_i - \mathbf{v}_j \right\| .$$

According to this validity function, minimising S corresponds to minimising J_s in eq. A1. An increase in the separation of the fuzzy *c*-partitions implies a larger value of $(d_{\min})^2$, thereby indicating that the minimal S is a valid optimal partition function.

The fuzzy deviation of x_k or y_k from partition i, d_{ik}, is

$$\text{(A4)} \quad d_{ik} = d(x_k, \mathbf{v}_i) = \left\| x_k - \mathbf{v}_i \right\| = \sqrt{\sum_{j=1}^{p} (x_{kj} - \mathbf{v}_{ij})^2}$$

where $\mathbf{v}_i = (\mathbf{v}_1, \mathbf{v}_2, ..., \mathbf{v}_c$ are the fuzzy centroids, determined using

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$$\text{(A5)} \quad v_i = \frac{\sum_{k=1}^{n} (\mu_{ik})^m x_k}{\sum_{k=1}^{n} (\mu_{ik})^m}.$$

A triangular fuzzy membership function, $\mu(x_k) = 1 - |x_k - v_i| / |v_i - (v_i - \Delta d_i)|$, was used to specify the fuzzy memberships of partition i, $\mu_{ik} \in [0,1]$ for x_k and y_k. Δd_i is the width of the membership function for either the left ($\Delta d_{i,L}$) or right ($\Delta d_{i,R}$) side of the centroid v_i. This allows the routine to determine asymmetric widths, where $\Delta d_{i,L} \neq \Delta d_{i,R}$.

The memberships μ_{ik} satisfy the conditions

$$\text{(A6}a\text{)} \quad \sum_{i=1}^{c} \mu_{ik} = 1, \quad 1 \leq k \leq n$$

$$\text{(A6}b\text{)} \quad \sum_{k=1}^{n} \mu_{ik} > 0, \quad 1 \leq i \leq c.$$

The first of these conditions ensures that the total membership of x_k, or y_k, over all partitions equals 1, while the second condition ensures that there are no empty partitions.

The FCM iteration scheme (see Kasabov 1996) initialises c fuzzy centroids, $v_i = (v_1, v_2, \ldots, v_c)$, and calculates the memberships, μ_{ik}, such that the conditions A6*a* and A6*b* are met. The centroids are then iterated according to eq. A5, and these next values for the centroids are used to update the fuzzy membership values, μ_{ik}, for each k according to

$$\text{(A7)} \quad \mu_{ik} = \left(\sum_{j=1}^{c} \left(\frac{d_{ik}}{d_{jk}} \right)^{\frac{1}{(m-1)}} \right)^{-1}, \quad \forall i$$

where $d_{ik} = (x_k - v_i)^2$ and $d_{jk} = (x_k - v_i)^2$ (Euclidean distances). Equation A7 implies the necessary condition that $d_{ik} > 0$, $\forall k$. If k is such that $d_{ik} = |x_k - v_i|^2 > 0$ for a given i, then following Bezdek et al. (1987), for all i, μ_{ik} are taken as any nonnegative numbers satisfying

$$\text{(A8)} \quad \sum_{i=1}^{c} \mu_{ik} = 1 \quad \text{and } \mu_{ik} = 0, \quad \text{if } d_{ik} \neq 0.$$

The iteration scheme continues until convergence of the centroid values for an optimal number of partitions, $c = c^*$, is achieved within the error criterion, ε, where for the $(l + 1)$th iteration, $|v_{i,l+1} - v_{i,l}| < \varepsilon$, and such that S in eq. A2 is minimised.

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PERSPECTIVES

Interindividual variation in the prolonged locomotor performance of ectothermic vertebrates: a comparison of fish and herpetofaunal methodologies and a brief review of the recent fish literature

A.S. Kolok

Abstract: Physiological research of locomotor performance in fishes has traditionally adopted an approach in which the mean performance of a number of fish was considered "real" and variation around the mean was considered statistical noise. Drawing on advances made in herpetofaunal studies, an alternative approach has recently appeared in the fish literature in which variation among individual fish has been shown to be repeatable and statistically valid. The incorporation, rather than suppression, of individual variation in experimental design has revealed interesting and biologically relevant relationships between morphological and physiological traits and swimming performance that can be masked by the traditional use of group means. Considering the promising nature of these initial studies incorporating individual variability in fish performance, this paper has two primary objectives. The first is to compare methodologies that have been used in studies involving intraspecific variability in the locomotor performance of fish and herpetofauna. The second is to review the fish literature regarding interindividual variation in prolonged swimming performance.

Résumé : Dans les recherches sur la performance locomotrice des poissons, on a dans le passé adopté une approche suivant laquelle la performance moyenne d'un ensemble de poissons était considérée comme « réelle » tandis que la variation autour de cette moyenne était considérée comme du bruit de fond statistique. Sur la base des progrès réalisés dans les études herpétofauniques, on a vu récemment apparaître dans la littérature sur les poissons une approche nouvelle suivant laquelle la variation inter-individuelle parmi les poissons s'avère reproductible et statistiquement valide. L'incorporation, plutôt que la suppression, de la variation individuelle dans les protocoles expérimentaux a mis en évidence l'existence de relations intéressantes et biologiquement pertinentes entre, d'une part, les caractères morphologiques et physiologiques et, d'autre part, la performance natatoire, relations qui peuvent être masquées par le recours classique aux moyennes de groupes. Inspiré par le caractère prometteur de ces premières études qui prennent en considération la variabilité individuelle dans la performance des poissons, le présent article poursuit deux grands objectifs. Premièrement, nous avons comparé les méthodes qui ont été utilisées dans les études prenant en compte la variabilité intraspécifique dans la performance locomotrice des poissons et de l'herpétofaune. Deuxièmement, nous avons passé en revue la littérature portant sur la variation inter-individuelle dans la performance natatoire des poissons sur de longues périodes.

[Traduit par la Rédaction]

Introduction

Swimming performances of fish have been classified into three major categories: sustained, prolonged, and burst (Beamish 1978). Sustained swimming performances are those that the fish can maintain for long periods (>200 min), whereas burst swimming performances are those that the fish can only maintain for very short periods (<20 s) of time. Prolonged swimming lasts between 20 s and 200 min, is primarily aerobic, and ends in fatigue. Arguably, prolonged swimming is the best studied form of fish locomotion, as the water velocities necessary to exercise the fish are reproducible in the laboratory with a swimming chamber and because fatigue (the inability of the fish to continue swimming) is a discrete, identifiable endpoint.

Although it is axiomatic that morphology and physiology will determine swimming performance, much research has been done to elucidate the exact relationships between mor-

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phological and physiological traits of the fish and swimming. Generally, the statistical approach used to make these inferences has been to compare mean performances of different groups of fish. Studies have been conducted that compare prolonged swimming performances of different species of fish (Fricke et al. 1987), the same species under different environmental conditions (Turnpenny 1983; Bernatchez and Dodson 1985), and the same individuals swimming at different water velocities (Kicenuik and Jones 1977; Thorarensen et al. 1996).

Prior to 1990, analysis of sample means was the predominant method used to analyze swim performance data. Variation in the performance of individual fish was rarely discussed, with the exception of the effect of body size on performance (e.g., see Brett 1965; Beamish 1978; Daxboeck 1981). Variation in the prolonged performance of similarly sized individuals was substantial enough to be mentioned in a few studies (e.g., Berry and Pimentel 1985; Watenpaugh and Beitinger 1985; Nelson 1989); however, no statistics were employed to examine this source of variability.

Since 1990, at least 15 studies have examined individual variation in prolonged swimming in relation to physiological and morphological traits (Table 1). While these papers are uncovering interesting and biologically relevant relationships between swimming performance and various morphological and physiological traits, it is difficult to interpret the studies as a collective body of knowledge because of differences in the methodologies employed in each study.

The methodologies necessary to standardize studies emphasizing interindividual variation in locomotor performance are available and have been used since the early 1980's by physiological ecologists working with reptiles and amphibians. The rationale for an interindividual approach is well presented in Bennett (1987). He reviewed publications that had established significant interindividual variation in locomotor performance and established that this performance variability was repeatable over time. He also reviewed literature suggesting that interindividual variation in performance can be correlated with variability in the physiology and morphology of the individuals involved. Since 1984, a number of studies involving amphibians and reptiles have concentrated on correlating physiological and morphological traits with variation in locomotor performance (Table 2).

The frequency of papers that deal with individual variability in the swim performance of fish is likely to increase over the next few years. Given this, fish biologists may want to seriously consider using methodologies employed by scientists working with reptiles and amphibians, prior to initiation of studies employing an individual approach. Thus, there are two primary objectives to this paper. The first is to compare the methodologies used in intraspecific studies involving fish and herpetofauna. The second is to conduct a brief review of the literature with respect to significant correlates between morphological and physiological traits of individual fish and swimming performance.

Prolonged performance: a critique of methodology

Critical swimming speed

In fish, the established measure of prolonged swimming performance is critical swimming speed (U_{crit}), in which the fish is forced to swim against an incrementally increasing flow of water until fatigue. Fatigue is defined as the point at which the fish can no longer maintain position in the chamber against the current and is impinged upon the rear grating of the swim chamber. In some studies, when fatigue is first noted, the fish is manually removed from the grating and reintroduced into the current (Gregory and Wood 1998), whereas in others the tail of the fish is gently prodded with a blunt probe to enduce the fish to move off the rear grid (Kolok et al. 1998). Although earlier studies used an electrical grid to keep the fish swimming (e.g., Kicenuik and Jones 1977), this practice violates many current animal care regulations, may unnecessarily stress the fish, and is currently in disfavor.

For those fish that do not fatigue exactly at the beginning or end of a prescribed swimming period, U_{crit} can be calculated as

$$U_{crit} = u_i + (t_i/t_{ii} \times u_{ii})$$

where u_i is the highest velocity maintained for the prescribed period (centimetres per second), u_{ii} is the velocity increment, t_i is the time (minutes) that the fish swam at the fatigue velocity, and t_{ii} is the prescribed period of swimming (minutes) (Brett 1964).

The U_{crit} can be expressed in absolute (centimetres per second) or relative (body length per second) terms (Table 1). Expression of the data in an absolute form is valuable, as it gives an estimate of the maximum velocity at which the fish can swim aerobically. If fish from a broad enough size range are examined, absolute U_{crit} generally scales positively with body size. Expression of the data in relative terms can also be valuable particularly when the fish vary substantially in body size and when the ultimate goal of the study is to emphasize swimming efficiency. Relative U_{crit} often scales negatively with body size, as smaller individuals swim more efficiently than do larger ones.

In contrast with absolute or relative U_{crit}, the most frequently encountered prolonged performance in the herpetofaunal literature is endurance (also called stamina). Endurance is usually the amount of time that the animal can run or crawl at an absolute speed (metres per second or kilometres per hour) (Table 2).

Even when measured on the same individuals, different measures of prolonged performance may or may not be directly comparable, as demonstrated by Kolok (1992*b*). In that study, the U_{crit} and endurance of winter- and summer-acclimatized juvenile largemouth bass (*Micropterus salmoides*) were determined. The endurance measurements for the winter-acclimatized fish were conducted at 15 cm·s^{-1} (75% of the mean U_{crit}), while the endurance measurements for the summer-acclimatized fish were conducted at 31 cm·s^{-1} (85% of the mean U_{crit}). Individual variability in U_{crit} was positively correlated with endurance in the winter-acclimatized fish but was not correlated with endurance in the summer-acclimatized fish. Furthermore, of the four physiological traits that correlated with U_{crit} in the winter-acclimatized fish, only one, heart cytochrome oxidase activity, was also correlated with endurance. Considering that variations in the aerobic performance measurement influence the results of intraspecific comparisons, it may be important to develop a stan-

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Table 1. List of papers published since 1990 that measured U_{crit}.

	Species	Paper	BM (g)	L (cm)	U_{crit}	BM/U_{crit} regression?	Variation in U_{crit}	t_{ii} (min)	u_{ii}	Correlated with?
1	*Cyprinodon pecosensis*	Kodric-Brown and Nicoletto 1993	1.14±0.04	2.7–3.8	cm·s^{-1}	Yes	Mean ± SE	3	2.9 cm·s^{-1}	Social status
2	*Fundulus grandis*	Kolok and Sharkey 1997	8.8±0.6	9.0±0.4	cm·s^{-1}	No	Correlation	20	5 cm·s^{-1}	Plasma osmolarity
			8.2±0.6	8.8±0.4						
3	*Gadus morhua*	Nelson et al. 1996	1000–1100	45–50	cm·s^{-1}	nt	Mean ± SE	30	10 cm·s^{-1}	Principal component analysis (see text)
4	*Gadus morhua*	Nelson et al. 1994	—	46.1±1.5	cm·s^{-1}	Yes	Range	30	10 cm·s^{-1}	None
			—	48.8±1.8						
5	*Micropterus salmoides*	Kolok 1992*a*	6.2–12.2	7.8–9.8	BL·s^{-1}	No	Rank order	20	5 cm·s^{-1}	None
			8.2–17.2	8.7–11.0						
6	*Micropterus salmoides*	Kolok 1992*b*	11.1±0.5	—	cm·s^{-1}, BL·s^{-1}	Yes	Histogram	20	5 cm·s^{-1}	14 traits
			12.7±0.5	—						
7	*Micropterus salmoides*	Kolok 1991	—	9.3–12.8	BL·s^{-1}	No	Mean ± SE	20	0.5 BL·s^{-1}	None
8	*Morone saxatilis*	Young and Cech 1993	13.7±0.3	8.5 (no variability given)	cm·s^{-1}	nt	Mean ± SE	2	10 cm·s^{-1}	None
			16.1±0.4							
			16.4±0.4							
			19.0±0.4							
9	*Oncorhynchus clarki*, *Oncorhynchus mykiss*	Hawkins and Quinn 1996	—	8.9±0.8	BL·s^{-1}	nt	Mean ± SE	15	0.25 BL·s^{-1}	None
			—	10.0±1.0						
10	*Oncorhynchus kisutch*	Farrell et al. 1997	11±0.25	9.6±0.2	cm·s^{-1}	nt	Mean ± SE	20	5 cm·s^{-1}	None
			121±8.4	22±1.2						
11	*Oncorhynchus mykiss*	Farrell et al. 1991	450–650		BL·s^{-1}	nt	Regression	20	0.2 BL·s^{-1}	Mucscle enzyme activity
12	*Oncorhynchus mykiss*	Farrell et al. 1990	545±22.5	—	cm·s^{-1}	nt	Mean ± SE	20	0.25 BL·s^{-1}	None
			618±19.9	—						
13	*Oncorhynchus mykiss*	Gallaugher et al. 1995	500±9	33–38	BL·s^{-1}	nt	Regression	30	1 BL·s^{-1}	Hematocrit
14	*Oncorhynchus mykiss*	Gallaugher et al. 1992	530–738	36–41	BL·s^{-1}	nt	Mean ± SE	10	10 cm·s^{-1}	Hematocrit
15	*Oncorhynchus mykiss*	Gregory and Wood 1999	4–8 g	—	cm·s^{-1}, BL·s^{-1}	Yes, no	Regression	40	0.75 BL·s^{-1}	Growth rate and six other traits
			—	8.3–10.5						
16	*Oncorhynchus mykiss*	Gregory and Wood 1998	18.7±1.0	—	cm·s^{-1}, BL·s^{-1}	Yes	Rank order	40	0.75 BL·s^{-1}	Growth rate and two other traits
			7.3–13.2	8.7–9.8						
17	*Oncorhynchus mykiss*	Keen and Farrell 1994	450±24	34.1±0.6	cm·s^{-1}, BL·s^{-1}	nt	Mean ± SE	20	8 cm·s^{-1}	None
			468±24	34.9±0.5						

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Table 1 (*concluded*).

	Species	Paper	BM (g)	L (cm)	U_{crit}	BM/U_{crit} regression?	Variation in U_{crit}	t_{li} (min)	u_{li}	Correlated with?
18	*Oncorhynchus mykiss*	Pearson and Stevens 1991	281±16	29.1±0.5	BL·s^{-1}	nt	Regression	15	10 cm·s^{-1}	Hematocrit, hemoglobin
			301±20	30.6±0.7						
19	*Oncorhynchus mykiss*	Thorarensen et al. 1996	401–1025	32–42	cm·s^{-1}, BL·s^{-1}	nt	None	30	0.25 BL·s^{-1}	None
20	*Oncorhynchus mykiss*	Wilson and Wood 1992	—	7.9±0.2	cm·s^{-1}, BL·s^{-1}	nt	Mean ± SE	60	6 cm·s^{-1}	None
				8.7±0.3						
21	*Oncorhynchus mykiss*	Wilson et al. 1994	5.85±0.8	9.0±0.3	BL·s^{-1}	nt	Mean ± SE	60	5 cm·s^{-1}	None
			8.59±1.2	9.7±0.3						
22	*Oncorhynchus mykiss*	Ye and Randall 1991	200–400	20–35	BL·s^{-1}	nt	Mean ± SE	30	0.5 BL·s^{-1}	None
23	*Oncorhynchus nerka*	Taylor and Foote 1991	—	7.0–8.5	cm·s^{-1}	Yes, no	Histogram	60	1 BL·s^{-1}	None
			—	8.6–10.0						
24	*Oncorhynchys tshawytscha*	Brauner et al. 1993	376±11	32±0.3	BL·s^{-1}	nt	Regression	30	20 cm·s^{-1}	Total functional hemoglobin
25	*Oncorhynchys tshawytscha*	Thorarensen et al. 1993	368±30	30.3±0.3	cm·s^{-1}	nt	Mean ± SE	15	0.5 BL·s^{-1}, 0.25BL·s^{-1}	None
			362±16	30.1±0.1						
26	*Pimephales promelas*	Kolok and Oris 1995	2.5±0.12	—	cm·s^{-1}	No	Range	20	5 cm·s^{-1}	Five traits related to growth
27	*Pimephales promelas*	Kolok et al. 1998	2.95±0.1	6.1±0.9	cm·s^{-1}	No	Mean ± SE	20	5 cm·s^{-1}	None
28	*Poecilia reticulata*	Nicoletto 1993	—	1.31–1.99	cm·s^{-1}	nt	None	3	2.9 cm·s^{-1}	Ornament complexity, orange area, number of orange spots
			—							
29	*Poecilia reticulata*	Nicoletto 1991	—	1.76±0.04	cm·s^{-1}, BL·s^{-1}	No	Mean ± SE	3	2.9 cm·s^{-1}	Tail type, dorsal fin length, carotinoid density
			—	1.75±0.05						
				1.73±0.05						
30	*Pomoxis annularis*	Parsons and Sylvester 1992	89–96	16.5–17.5	cm·s^{-1}	nt	Range	30	5 cm·s^{-1}	None
31	*Pytocheilus oregonensis*	Kolok and Farrell 1994*a*	315±15	30.9±0.7	cm·s^{-1}	No	Rank order	20	10 cm·s^{-1}	8 cardiovascular traits
			164±14.5	25.0±0.7						
32	*Pytocheilus oregonensis*	Kolok and Farrell 1994*b*	179–424	26.6–34.1	cm·s^{-1}	No	Mean ± SE	20	10 cm·s^{-1}	None
33	*Salmo trutta*	Butler et al. 1992	320–520	30–46	cm·s^{-1}, BL·s^{-1}	nt	Mean ± SE	15	100 cm·s^{-1}	None

Note: The table includes species used, body mass (BM) and length (L), expression of U_{crit} (body lengths (BL)·s^{-1} or cm·s^{-1}), whether or not a BM/U_{crit} regression was statistically significant (yes, no, or not tested (nt)), information given with respect to degree of individual variation in U_{crit}, numerical values for t_{li} and u_{li} (see text), and the morphological and physiological factors correlated with U_{crit} (if any). Studies are presented alphabetically by species.

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Table 2. List of papers published since 1984 that measured the treadmill endurance performance of amphibians and reptiles.

Species	Paper	Taxon	BM (g)	*L* (cm)	Endurance	Velocity increment	BM/endurance regression?	Multiple regression	Principle component analysis
Ambystoma tigrinum nebulosum	Bennett et al. 1989	Salamander	3.2–23.8	—	Variable	0.05 km·h^{-1}	Yes	Yes	Yes
Amphibolurus nuchalis	Garland and Else 1987	Lizard	1.3–50	—	1 km·h^{-1}	None	Yes	Yes	Yes
Amphibolurus nuchalis	Garland et al. 1987	Lizard	17.0–41.2 16.3–43.7	—	1 km·h^{-1}	None	Yes	No	No
Bufo marinus	Longphre and Gatten 1994	Toad	20.4–57.0	6.8–9.0	Variable	0.1 km·h^{-1}	No	Yes	No
Ctenosaura similis	Garland 1984	Lizard	12.3–866	—	1 km·h^{-1}	None	Yes	Yes	No
Sceloporus occidentalis	Garland et al. 1990*a*	Lizard	4–13.2	5.0–7.4	0.5 km·h^{-1}	None	Yes	No	No
Thamnophis sirtalis	Garland et al. 1990*b*	Snake	1.22–3.34	16.0–20.7	0.3 km·h^{-1}	None	Yes	Yes	No
Thamnophis sirtalis	Jayne and Bennett 1990	Snake	—	—	0.5 km·h^{-1}	None	Yes	No	No

Note: The table includes species, taxon, body mass (BM) and length (*L*), treadmill velocity at which endurance was measured (endurance), increments (if any) at which the treadmill velocity was increased, whether a regression analysis was conducted between body mass and the locomotor performance, and whether multiple regression and (or) principle component analysis was used to analyze the data.

dardized protocol for U_{crit} to enhance comparability of results from one study to the next.

A standard protocol for U_{crit} has not been accepted by fish physiologists. In the literature, the magnitude of the velocity increments (u_{ii}) and the prescribed time interval for each swimming period (t_{ii}) vary considerably (Table 1). These variations are important, as they can profoundly influence U_{crit} (Farlinger and Beamish 1977) and by extension can profoundly influence the results of intraspecific studies. In most published studies (Table 1), u_{ii} ranges between 5 and 10 cm·s^{-1}, which is consistent with the velocity increment of 10 cm·s^{-1} recommended by Beamish (1978). Obviously, the velocity increment to be used will have to be adjusted for very large or very small fish. In addition, t_{ii} is generally between 10 and 30 min; however, prescribed periods much greater (60 min) and less (2 min) have been used. Using a t_{ii} of less than 20 min will almost certainly lead to an increase in U_{crit}, while the use of a t_{ii} greater than 30 min may or may not lead to a decrease in U_{crit} (Brett 1967; Farlinger and Beamish 1977). Use of a u_{ii} or a t_{ii} that is very different from the standards of 5–10 cm·s^{-1} and 20–30 min, respectively, may subject the fish to performances that are energetically more like burst or sustained performances than a standard U_{crit}. Intraspecific studies featuring an uncommon u_{ii} or t_{ii} will not be comparable with the rest of the literature in this field and as such may have limited utility.

Another inconsistency associated with the U_{crit} measurement is that the water velocity increment (u_{ii}) has been expressed in both absolute (centimetres per second) and relative (body lengths per second) terms (Table 1). Implementing a u_{ii} that covaries with body size may be appropriate if there is a large variability in the size range of the fish used in the experiment. Generally, however, variation in body size is relatively narrow in most fish studies (Table 1), precluding the necessity of size adjusting u_{ii}. Furthermore, even in studies employing a wide variation in body size, size adjustment of u_{ii} may not be necessary. For example, Brett (1965) determined the prolonged swimming performance of sockeye salmon (*Oncorhynchus nerka*) ranging in mass from 3.38 to 1432 g, and a u_{ii} of 9.1 cm·s^{-1} was successfully used for all individuals.

In the herpetological literature, intraspecific comparisons of the endurance of different species of reptile and amphibian often feature individuals that vary widely in body mass (e.g., the size variation found in Garland (1984) and Garland and Else (1987) is in excess of one order of magnitude). In these studies the treadmill velocity for the endurance test does not vary from one individual to the next but rather is constant for all individuals.

Performance repeatability

Analysis of individual variation in locomotor performance is futile if the performances are not repeatable. Repeatability of performance can be demonstrated by conducting multiple performance tests on a number of individuals and then statistically testing for repeatability with either a Spearman rank correlation coefficient or a Kendall coefficient of concordance (e.g., see Bennett 1980). Repeatability has been demonstrated in this fashion for lizards, snakes, and amphibian burst performance, endurance, and antipredator behavior (Table 3). Most of these studies measured performance re-

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Table 3. Studies demonstrating performance repeatability in fishes, amphibians, and reptiles.

Species	Study	Performance	Comments
Fish			
Gadus morhua	Nelson et al. 1994	U_{crit}	
Micropterus salmoides	Kolok 1992*a*	U_{crit}	Acute temperature change
Micropterus salmoides	Kolok 1992*b*	U_{crit}, endurance	
Oncorhynchus mykiss	Gregory and Wood 1999	U_{crit}	
Oncorhynchus mykiss	Gregory and Wood 1998	U_{crit}, endurance	Fish in schools of up to 10
Pimephales promelas	Kolok et al. 1998	U_{crit}	
Pytocheilus oregonensis	Kolok and Farrell 1994*a*	U_{crit}	
Reptiles and amphibians			
Agama savignyt, *Stellio stellio*	Huey and Hertz 1984	Burst speed	Lizard, acute temperature change
Amphibolurus nuchalis	Garland and Else 1987	Endurance, maximal aerobic speed	Lizard
Amphibolurus nuchalis	Garland 1985	Maximum speed	Lizard
Bufo woodhousei fowleri	Walton 1988	Sprint speed, sustained speed	Toad
Cnemidophorus murinus, *Dipsosaurus dorsalis*, *Eumeces obsoletus*, *Gerrhonotus multicarinatus*, *Sceloporus occidentalis*, *Uma inornata*	Bennett 1980	Burst speed, distance running capacity	Lizard
Dipsosaurus dorsalis	Gleeson and Harrison 1988	Burst speed	Lizard
Sceloporus merriami	Huey and Dunham 1987	Sprint speed	Lizard
Sceloporus occidentalis	Garland et al. 1990*a*	Sprint speed	Lizard
Thamnophis sirtalis	Garland 1988	Endurance, burst speed, antipredator behavior	Snake
Thamnophis sirtalis fitchi	Garland et al. 1990*b*	Maximum speed, endurance	Snake

Note: The table includes species and type of performance. For the fish species, the comments refer to any unusual treatment; for the reptiles and amphibians, the comments delineate the type of animal involved in the study.

peatability in two or more trials days or weeks apart under consistent abiotic conditions. Huey and Hertz (1984) demonstrated that the rank order of burst performance of two lizard species was significantly repeatable following changes in body temperature, whereas Huey and Dunham (1987) demonstrated that sprint speed was repeatable in wild populations of the lizard *Sceloporus merriami* up to 1 year after the first bout of performance (also see Van Berkum et al. 1989; Jayne and Bennett 1990).

In fish, performance repeatability of U_{crit} has been documented in at least seven studies involving five species (Table 3). It has been demonstrated for fish in which the abiotic and biotic environments have not changed between performance trials (Kolok 1992*a*, 1992*b*; Nelson et al. 1994; Gregory and Wood 1998; Kolok et al. 1998). It has also been demonstrated for largemouth bass following an acute drop in water temperature of 10°C (Kolok 1992*a*) and for northern squawfish (*Ptychocheilus oregonensis*) following surgical implantation of a flow probe around the ventral aorta (Kolok and Farrell 1994*a*). Performance repeatability has also been documented for endurance in largemouth bass (Kolok 1992*b*) and juvenile rainbow trout (*Oncorhynchus mykiss*) (Gregory and Wood 1998). The Gregory and Wood (1998) study demonstrated repeatability of U_{crit} for rainbow trout swimming alone and in small groups of 10 or less. The utility of swimming small groups of fish in studies emphasizing individual variation in performance is likely to be limited to strong swimmers (such as salmonids) that routinely partake in schooling behavior. Furthermore, while it has been demonstrated that schooling imparts a significant benefit to the swim performance of members of a school (Beamish 1978; Lindsey 1978), it remains to be determined whether a poor-performing individual can enhance its performance capabilities by maintaining an advantageous position within a fish school. More research will be necessary to clarify the effect of schooling on the repeatability of U_{crit} for individual fish.

Body size

The importance of body size as a trait that can influence the locomotor performance of animals has been recognized for almost as long as the measurements have been made. The size range of lizards and amphibians used in studies featuring an interindividual approach is often quite large (greater than an order of magnitude, Table 2), although there have been exceptions when only juveniles (Garland 1988) or only adults (Longphre and Gatten 1994) were studied. In all cases, size adjustment of endurance performance was done by regressing body mass with endurance performance (usually log body mass is regressed against log performance) and then by conducting additional analysis on the regression residuals.

In fish the situation is quite different. While the relationship between body size and swim performance is also allometric, this relationship has rarely been determined

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experimentally (for an exception, see Brett 1965). Generally, size variation among individual fish used in most studies is narrow, and the relationship between fish size and U_{crit} is rarely a major focus of the study. Fish are often obtained from hatcheries where the animals are all of similar size or the fish are preselected for similarities in body size. For example, in 33 recent studies (post-1989) in which U_{crit} has been measured, variation in body mass or length is frequently less than 10% of the mean (Table 1).

In the fish literature, U_{crit} has been size adjusted in two different ways: either by generation of a mass or length index (e.g., body lengths per second) or by expressing the data in absolute terms (centimetres per second), regressing them against body mass or length, and then analyzing regression residuals. If size adjustment is undertaken solely to remove size variation from the data set, then regression residual analysis of absolute U_{crit} is preferable to the use of a mass or length index for at least two major reasons. First of all, the use of an index to size adjust performance data implies that the size versus U_{crit} relationship is isometric (i.e., it has zero as its *y*-intercept, and an incremental increase in size will lead to the same incremental increase in U_{crit}, Packard and Boardman 1987, 1988). These assumptions are not generally met. Size adjustment of U_{crit} data with a mass or length index may obfuscate the true relationship between fish size and U_{crit} and may also alter the non-size-related variation in U_{crit} that exists among similarly sized individual fish.

A second problem with the use of an index to size adjust is that an index size adjusts the data set whether or not it is necessary. If absolute U_{crit} is not correlated with body mass or length, then size adjustment is unnecessary. In Table 1, none of the nine studies that used body length per second size-adjusted data tested whether a significant relationship between length and absolute U_{crit} existed prior to size adjustment (Kolok (1991, 1992*a*) regressed relative, but not absolute, U_{crit} against length). Obviously, the largest fish in a population will be able to swim faster than small juveniles; however, if the size range of the fish is narrow (which is often the case), size adjustment may be unnecessary (e.g., see Kolok and Farrell 1994*a*; Kolok and Oris 1995; Kolok and Sharkey 1997). It is most prudent to check for size-related variability in the data by regressing absolute U_{crit} against either body mass or body length. If a significant relationship between size and U_{crit} exists, then the data will need to be size adjusted, preferably using regression residuals.

Review of studies correlating morphological and physiological traits with swimming performance

Despite the differences in methodology mentioned above, studies in which the morphology and physiology of individual fish are correlated with variation in U_{crit} are appearing with greater frequency in the literature. A brief review of the findings and statistical methodologies used in these studies is given below. Results from the herpetofaunal literature are briefly discussed from a methodological perspective.

Simple linear regression

Regression analysis can be used to answer the question of whether a statistically significant relationship exists between variation in a morphological or physiological trait and variation in locomotor performance. Simple linear regression involving one trait and one performance variable is one of the simplest types of regression analysis and is the most common in the fish literature.

Oxygen consumption

Considering that U_{crit} is primarily an aerobic performance, it is interesting to note that individual variation in U_{crit} has not been correlated with maximum oxygen consumption or metabolic scope for activity (maximum minus standard metabolic rate) in any study involving fish. In the herpetofaunal literature, maximum oxygen consumption was found to be significantly correlated with endurance in the snake *Thamnophis sirtalis* (Garland and Bennett 1990) and the lizard *Ctenosaura similis* (Garland 1984). In contrast, maximum oxygen consumption was not correlated with endurance in the lizard *Amphibolurus nuchalis* (Garland and Else 1987) or with maximum aerobic speed of the toad *Bufo marinus* (Longphre and Gatten 1994). Research into the relationship between individual variation in oxygen consumption and fish performance may prove to be particularly insightful and is an area that merits study.

Hematological traits

Simple linear regression has been conducted on the relationship between U_{crit} and hematocrit (Gallaugher et al. 1992, 1995), total functional hemoglobin (Brauner et al. 1993), and hematocrit and hemoglobin (Pearson and Stevens 1991). In each case, experimental manipulation of the fish was conducted to expand variation in the hematological traits beyond that existing in normal, healthy fish. In no case did any of the hematological traits correlate with U_{crit} when restricted to a range found in healthy fish. These results are consistent with the recent findings of Gregory and Wood (1999), which did not show any significant correlations between hematocrit and U_{crit} in juvenile rainbow trout fed rations varying from 0.5 to 2.0% wet body mass·day^{-1}.

Plasma osmolarity

Kolok and Sharkey (1997) regressed plasma osmolarity against the U_{crit} of gulf killifish (*Fundulus grandis*). They found a significant regression between these two traits for fish in freshwater, where gulf killifish are osmotically stressed, but no statistically significant relationship for the fish in brackish water.

Muscle enzymatic activity

Farrell et al. (1991) found positive regressions between U_{crit} and red muscle and endocardial muscle glutamate dehydrogenase and hydroxylacyl CoA dehydrogenase in rainbow trout. Each regression analysis included data from trained (n = 5) and untrained (n = 5) fish. It is unclear, given the small sample size, whether a significant relationship would have existed between enzymatic activity and U_{crit} if the trained or untrained fish were analyzed independently. Nevertheless, a similar result to that of Farrell et al. (1991) was found by Kolok (1992*b*): red and cardiac muscle cytochrome oxidase activity was significantly correlated with U_{crit} in winter-acclimatized juvenile largemouth bass.

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Growth and traits associated with Darwinian fitness

It has been found that enzymatic activities are often positively correlated with growth rate (Goolish and Adelman 1987; Mathers et al. 1992), and because some enzymatic activities have been shown to be positively correlated with U_{crit} (see previous paragraph), it is tempting to suggest that a positive correlation exists between growth and U_{crit}. The relationship between growth rate and U_{crit}, however, is more complex. For example, Kolok and Oris (1995) found that the relationship between growth rate and absolute U_{crit} was negative in subadult male fathead minnows (*Pimephales promelas*) (i.e., faster growing individuals had a reduced U_{crit}). This result is consistent with the results of Gregory and Wood (1998) in which they found a negative correlation between growth rate and relative U_{crit} (body lengths per second) in juvenile rainbow trout fed a half-satiation ration but no significant correlation between the two traits in fish fed to satiation. In a follow-up study (Gregory and Wood 1999), they found a negative correlation between growth rate and relative U_{crit} in fish fed a ration of 2.0% wet body mass· day^{-1}, no correlation in fish fed a ration of 1.5 and 1.0% wet body mass·day^{-1}, and a positive correlation between the two in fish fed at 0.5% wet body mass·day^{-1}.

Although growth rate is negatively correlated with U_{crit} unless rations are restricted, significant correlates exist between U_{crit} and other traits associated with Darwinian fitness. For example, Nicoletto (1991) found positive correlations between the density of carotenoid pigments and U_{crit} in male guppys (*Poecilia reticulata*). In Nicoletto (1993), positive correlations were found between U_{crit} and male displays, as well as the total area and number of orange spots on the fish. These results are consistent with the results of Kodric-Brown and Nicoletto (1993): male Pecos pupfish (*Cyprinodon pecosensis*) that were brightly colored and territorial had significantly greater U_{crit} than males that were nonterritorial.

Size adjustment of morphological and physiological traits

When a relatively large number of morphological and physiological traits are all measured on the same individuals, statistical analysis can become more sophisticated than determining simple linear regressions between a single trait and prolonged performance. Prior to conducting regression analysis, however, it is often necessary to size adjust the morphological and physiological data. In the herpetofaunal literature, the influence of body size is generally removed from the data by using regression residuals from the linear relationship between the physiological or morphological trait and the body length or mass. For example, Longphre and Gatten (1994) made measurements of 12 morphological and physiological traits (excluding body mass and length) on the toad *Bufo marinus*. Many of these measurements were size dependent, and the influence of body size was removed by using regression residuals. Significant regressions were found between body length and femur length, tibiofibular length, foot length, and leg length; in addition, significant regressions were found between body mass and steady-state oxygen consumption, ventricle mass, condition index, gastrocnemius mass, and iliofibularis mass.

In the fish literature, a few studies have size adjusted physiological and morphological traits and then used these data to conduct regression residual analysis. For example, size variation was removed from liver mass and heart mass of juvenile largemouth bass with regression residuals via regressions of these traits with body mass (Kolok 1992*b*). Similarly, in the same study, size variation in red muscle cross-section area (from a cross section of the caudal peduncle) was removed by using regression residuals from the regression of these traits with total cross-section area (Kolok 1992*b*). Regression residual analysis has also been used to remove size variation from cardiovascular data (e.g., maximum stroke volume, maximum cardiac output; Kolok and Farrell 1994*a*; Thorarensen et al. 1996). Interestingly, in the case of these cardiovascular traits, size adjustment with an index (i.e., expressing cardiac output as millilitres per minute per kilogram rather than millilitres per minute) may be acceptable, as these relationships appear to be isometric (see Thorarensen et al. 1996).

Multiple regression, principle component analysis, and partial correlation analysis

In the herpetofaunal literature, studies correlating morphological and physiological traits with endurance performance have employed multiple regression analysis (Garland 1984; Garland and Else 1987; Bennett et al. 1989; Garland and Bennett 1990; Longphre and Gatten 1994) and principle component analysis (Garland and Else 1987; Bennett et al. 1989). If the morphological and physiological traits measured are not strongly intercorrelated, then multiple regression is probably the preferred method for statistical analysis. If, however, the traits are strongly intercorrelated, then data from some of the traits will supply redundant information, which will create numerical difficulties in estimating the parameters in regression equations. If this situation exists, then one of a number of techniques must be used to reduce intercorrelation of the traits, including principal component analysis (Slinker and Glantz 1985).

Since 1990, statistical approaches used to analyze interindividual variation in U_{crit} have become more sophisticated. Instead of simple linear regressions being conducted, attempts have been made to determine the effect of multiple traits on U_{crit}. Three approaches have been used: multiple regression, principle component analysis, and partial correlation. A brief review of the findings of each of these studies follows.

Multiple regression

Two studies have been conducted in which multiple regression has been applied to U_{crit} data. Kolok (1992*b*) conducted a study in which 14 morphological and physiological traits were measured along with U_{crit} in winter- and summer-acclimatized juvenile largemouth bass. The physiological and morphological traits featured tissue masses and enzymatic activities. A correlation matrix was presented to address the intercorrelation of the measured variables, which was relatively minor. Simple regressions were determined for U_{crit} and endurance with a number of traits being either positively or negatively correlated with performance. A forward stepwise multiple regression was then conducted on the traits and performance.

One of the significant findings of Kolok (1992*b*) was that heart cytochrome oxidase activity was positively correlated

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with swim performance. With that result in mind, Kolok and Farrell (1994*a*) conducted a correlational analysis of cardiovascular traits and U_{crit} in winter- and summer-acclimatized northern squawfish. A correlational matrix of the traits was given, and there were strong intercorrelations between body mass, heart mass, maximum stroke volume, maximum cardiac output, and scope for cardiac output. These data were size adjusted using regression residuals and the residuals correlated with U_{crit} for both the summer- and winter-acclimatized fish. No significant correlations were found between U_{crit} and the cardiovascular variables.

Principle component analysis

Since 1990, there have been at least three studies that have used principle component analysis to address how well variation in morphological and physiological traits explains variation in U_{crit} (Taylor and Foote 1991; Hawkins and Quinn 1996; Nelson et al. 1996). Taylor and Foote (1991) measured 10 morphological traits (modified truss measurements to compare overall body depth and length and depth of the caudal region) in sockeye salmon and kokanee (*Oncorhynchus nerka*), whereas Hawkins and Quinn (1996) measured the same 10 traits in cutthroat trout (*Oncorhynchus clarki*), steelhead trout (*Oncorhynchus mykiss*), and their hybrids. In Taylor and Foote (1991), morphological data were not size adjusted prior to inclusion in the principal component analysis, and the first component was significantly correlated with fish length. The second and third components, however, were considered to be indicative of morphological variation independent of body size. In contrast, Hawkins and Quinn (1996) used data that were size adjusted (using an allometric equation) prior to inclusion in the principal component analysis. In both cases, results of the analysis indicate that the best-swimming fish had a morphology different from that of the poorer swimmers. For example, in both studies, fish with longer caudal regions tended to be better swimmers.

Nelson et al. (1996) analyzed the relationship between physiological characteristics and U_{crit} in Atlantic cod (*Gadus morhua*) from two different populations. The data were not size adjusted prior to the analysis, nor was there any mention of whether or not the measured traits varied allometrically. Considering that the traits were hematological and physiological in nature, there were no a priori reasons to assume allometry in the relationship between the traits and performance. The second component strongly correlated with U_{crit} and was an amalgam of blood oxygen-carrying capacity, cardiovascular capacity, and stress level of the fish prior to the experiment.

Partial correlation analysis

Partial correlation analysis is used to determine whether the correlation between two variables is attributable to a correlation with a third variable. For example, Nicoletto (1993) found significant correlations between U_{crit} and rates of display, orange area, orange spot number, and ornament complexity in the guppy. Some of these traits may have only been correlated with U_{crit} indirectly because they were correlated with a third trait that was directly correlated with U_{crit}. To determine whether this was the case, Nicoletto (1993) conducted partial correlations and found significant correlates between U_{crit} and ornament complexity, rate of display, and orange area after removal of variability due to other covariates. The resultant data suggest that ornament complexity, display frequency, and orange area are independently significant correlates of U_{crit} despite intercorrelations between the traits.

Conclusions

Considering how few studies on U_{crit} have emphasized differences among individuals, generalizations are, at best, preliminary. On the positive side, where individual variation in U_{crit} has been measured, it has been found to be substantial and repeatable, suggesting that the approach is valid. Unfortunately, variations in the performance measurement (e.g., measuring endurance rather than U_{crit}) will alter the physiological and morphological traits that correlate with prolonged swimming (Kolok 1992*b*). While endurance is rarely measured in studies involving fish, absolute and relative U_{crit} are both frequently measured prolonged performances, and it is likely that traits correlating with absolute U_{crit} may be very different from traits that correlate with relative U_{crit}. Given the statistically sophisticated methods available to size adjust absolute U_{crit}, it is probably most appropriate for intraspecific correlational studies with fish to feature this performance measurement.

Despite the methodological dissimilarities among studies that have featured correlative analysis, some generalizations can be made. Factors associated with Darwinian fitness (e.g., coloration, male territoriality) have been shown to be positively correlated with U_{crit}. Growth rate would also appear to be a factor associated with Darwinian fitness, as larger fish have been shown to be socially dominant (Abbott et al. 1985) and to have preferential access to food (Fausch 1983; Metcalfe 1986). Despite these benefits, the relationship between U_{crit} and growth rate is negative (Kolok and Oris 1995; Gregory and Wood 1998, 1999). How faster growth can simultaneously provide social advantages to individual fish and reduce their U_{crit} is an issue that merits further study.

Another interesting result that has been identified is the lack of strong correlations between U_{crit} and physiological traits associated with oxygen transport (Gallaugher et al. 1992, 1995; Brauner et al. 1993) and cardiac output (Kolok and Farrell 1994*a*, 1994*b*). These results were from fish that are very good swimmers (rainbow trout and northern squawfish), yet results from more sluggish fish species (see Kolok 1992*b*; Nelson et al. 1996) suggest that there may be significant relationships between cardiovascular performance, oxygen delivery, and U_{crit}. Additional studies on individual variability in the cardiovascular and swimming performance of active and sluggish fish species will be necessary to elucidate these relationships.

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Why did the Prince William Sound, Alaska, Pacific herring (*Clupea pallasi*) fisheries collapse in 1993 and 1994? Review of hypotheses

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Abstract: Following record harvests of Pacific herring (*Clupea pallasi*) in Prince William Sound, Alaska, in the 3 years after the *Exxon Valdez* oil spill, the fishery failed in 1993. The hypotheses advanced to explain this dramatic 1993 decline occur in three categories: (*i*) effects associated with the 1989 oil spill, (*ii*) harvesting effects, and (*iii*) natural phenomena. Based on our review, we are convinced that a combination of increasing Prince William Sound herring biomass and decreasing food supply led to poor condition of Prince William Sound herring, which resulted in the 1993 decline. Other natural causes could have contributed to the decline, including disease, cold water temperatures, increased predation, and other natural stochastic processes. No evidence supports hypotheses that the decline resulted solely from overharvesting or underharvesting. The record high population levels and harvests of Prince William Sound herring in the years after the 1989 oil spill, the lack of change from the expected age-class distribution, and the low level of oil exposure documented for herring in 1989 and the following years all indicate that the 1989 oil spill did not contribute to the 1993 decline. Poor nutritional status, either alone or in combination with disease or other natural factors, was most likely responsible for the 1993 collapse.

Résumé : Après les prises records de hareng du Pacifique (*Clupea pallasi*) dans la baie du Prince William, en Alaska, dans les 3 années qui ont suivi le déversement d'hydrocarbures de l'*Exxon Valdez*, cette pêche s'est effondrée en 1993. Les hypothèses avancées pour expliquer ce déclin dramatique de 1993 sont de trois ordres : (*i*) effets du déversement de 1989, (*ii*) effets de la pêche et (*iii*) phénomène naturel. Après examen des données existantes, nous sommes convaincus que l'accroissement de la biomasse de hareng dans la baie combinée à la baisse des ressources alimentaires ont affecté l'état du hareng dans cette région, d'où le déclin de 1993. D'autres causes naturelles ont pu contribuer à ce déclin, dont la maladie, les basses températures de l'eau, un accroissement de la prédation et d'autres processus stochastiques naturels. Rien ne laisse penser que le déclin serait dû exclusivement à la surpêche ou à une sous-exploitation de la ressource. La population et les prises records de hareng dans les années qui ont suivi la marée noire de 1989, l'absence de changement dans la distribution attendue des classes d'âge et la faible exposition du hareng aux hydrocarbures signalée en 1989 et dans les années suivantes indiquent que le déversement de 1989 n'est pas responsable du déclin des prises en 1993. L'effondrement de 1993 a probablement été causé par un manque de ressources alimentaires, combiné ou pas avec la maladie ou d'autres facteurs naturels.

[Traduit par la Rédaction]

Introduction

Pacific herring (*Clupea pallasi*) are an important resource in Prince William Sound (PWS), Alaska, in terms of both their commercial harvest (Donaldson et al. 1993) and their role as a fodder fish (Livingston 1995). In 1989, there was no commercial harvest following the *Exxon Valdez* oil spill (EVOS); however, during the period 1990–1992, there was first an above-average commercial herring harvest in PWS followed by two record-high harvests (Fig. 1). The strong recruitment of the 1988 year-class supported the record biomass and harvest in 1992. An all-time record-high biomass of 134 000 t (all units are short tons (2000 pounds) except in Table 1 where t represents metric tons) was predicted for 1993 (Funk 1993) but did not materialize. In the 1993 spring fisheries, an estimated 30 000 t of herring was observed, a lower than expected biomass (Brown et al. 1994). No 1993 purse-seine fishery occurred, and the 1993 gillnet fishery, historically a small portion of the commercial harvest, was about 1100 t, slightly over quota. The overall 1993 PWS herring harvest was only 14% of the 1992 harvest of 26 267 t (Fig. 1). In 1993, external lesions were observed in about one third of

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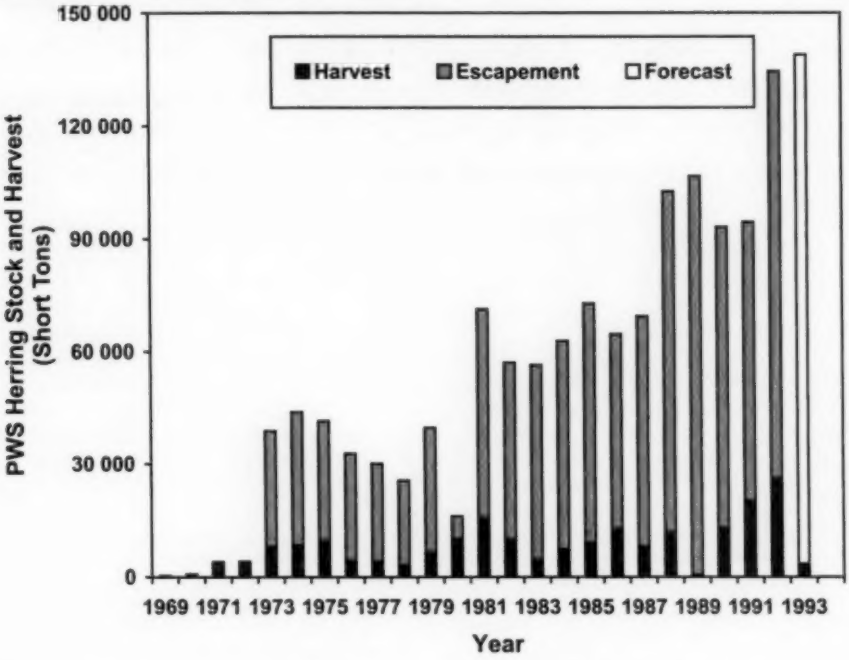
Fig. 1. Biomass and harvests of Pacific herring in PWS, 1969–1993.



herring samples from PWS (Brown et al. 1994), and viral hemorrhagic septicemia virus (VHSV) was isolated from PWS herring (Meyers et al. 1993).

The 1993 collapse carried longer term implications. Because the fishery typically exploits fish from 3+ to 9 years of age, it was estimated that 3–4 years would be needed to provide sufficient recruitment to again support a commercial fishery. Indeed, in 1994, the herring biomass was again low. An estimated 20 000 t of herring was observed in 1994 by the Alaska Department of Fish and Game (ADFG) (Brown et al. 1994), and the PWS spring fisheries were not opened. Also in 1994, external lesions and VHSV were observed on PWS herring but were not as prevalent or as intense as those observed in 1993. For lack of sufficient biomass, the spring herring fisheries in PWS also did not open in 1995 or 1996. Small spring fisheries occurred in PWS in 1997 and 1998, amounting to 4883 t and 3843 t, respectively. The hypotheses to explain the dramatic 1993 decline of PWS herring can be placed into three general categories: (*i*) those postulating a causal connection to the 1989 oil spill, (*ii*) those suggesting harvesting effects, and (*iii*) those attributing the decline to natural phenomena.

This paper reviews the hypotheses concerning the ultimate cause or causes of the 1993 PWS herring decline. Before reviewing the hypotheses, we provide a background on the PWS herring population. Because the potential exposure of PWS herring to oil from the EVOS pertains directly to one set of hypotheses, we also describe the spill events and potential for exposure of herring life stages to the oil spill. We then list the major hypotheses with their variants and examine the evidence associated with each major hypothesis. We argue that the evidence is most consistent with the hypothesis that the 1993 PWS herring decline resulted from a combination of natural factors.

Background on PWS herring

PWS herring start to recruit to the spawning biomass at age 3 and are not fully recruited until age 5 or 6 (Funk 1993). Since the early 1970's, when the PWS sac-roe herring fisheries began, herring fishery harvests and herring biomass within PWS have generally been increasing (Figs. 1 and 2). Different measures have been used over the years to indicate the abundance of herring in PWS. However, the ADFG used an age-structured analysis (ASA) (Funk 1993) to synthesize the available data and clearly demonstrated that during the era of sac-roe fisheries, the highest biomass levels in PWS have been seen since 1988, when the strong 1984 and 1988 year-classes recruited to the spawning population (Fig. 3). Analyses of data from the 1970's onward show that a strong year-class recruits to the PWS and other Gulf of Alaska (GOA) herring populations about every 4 years (Funk 1993; Funk and Sandone 1990). The commercial fishery is then supported by the presence of this major year-class for several years until the next major year-class recruits, usually at 4-year intervals (Fig. 3).

Overview of the 1989 oil spill

On March 24, 1989, the *Exxon Valdez* grounded on Bligh Reef, releasing about 260 000 barrels (42 000 000 L) of Alaska North Slope (ANS) crude oil into PWS (Brown et al. 1996). From Bligh Reef in northeastern PWS, the oil slick moved generally southwest, grounding on beaches in the Naked Is-

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Fig. 2. Ex-vessel value of annual harvest of Pacific herring in PWS.

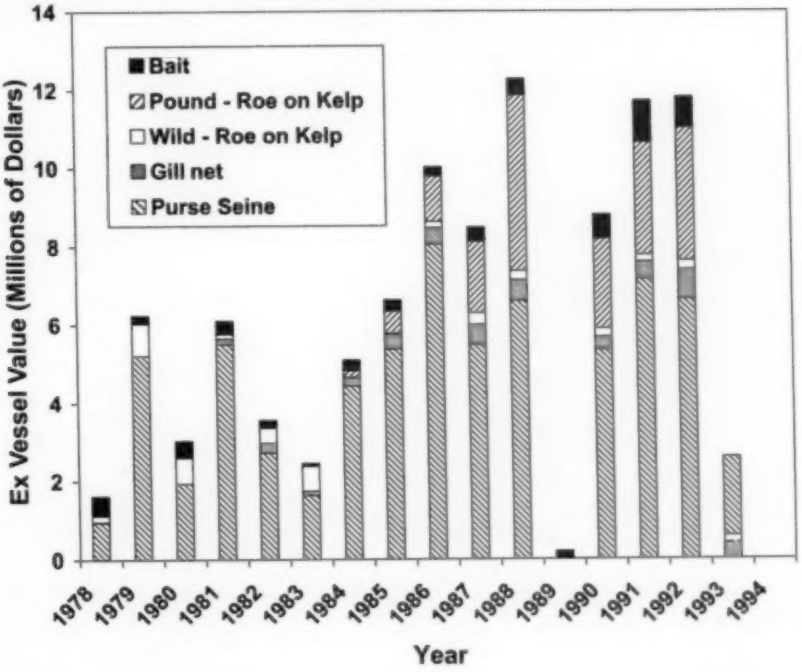

Fig. 3. Year-class distribution of Pacific herring in PWS, 1987–1994 (1994 values are from the ADFG spawning biomass estimate).

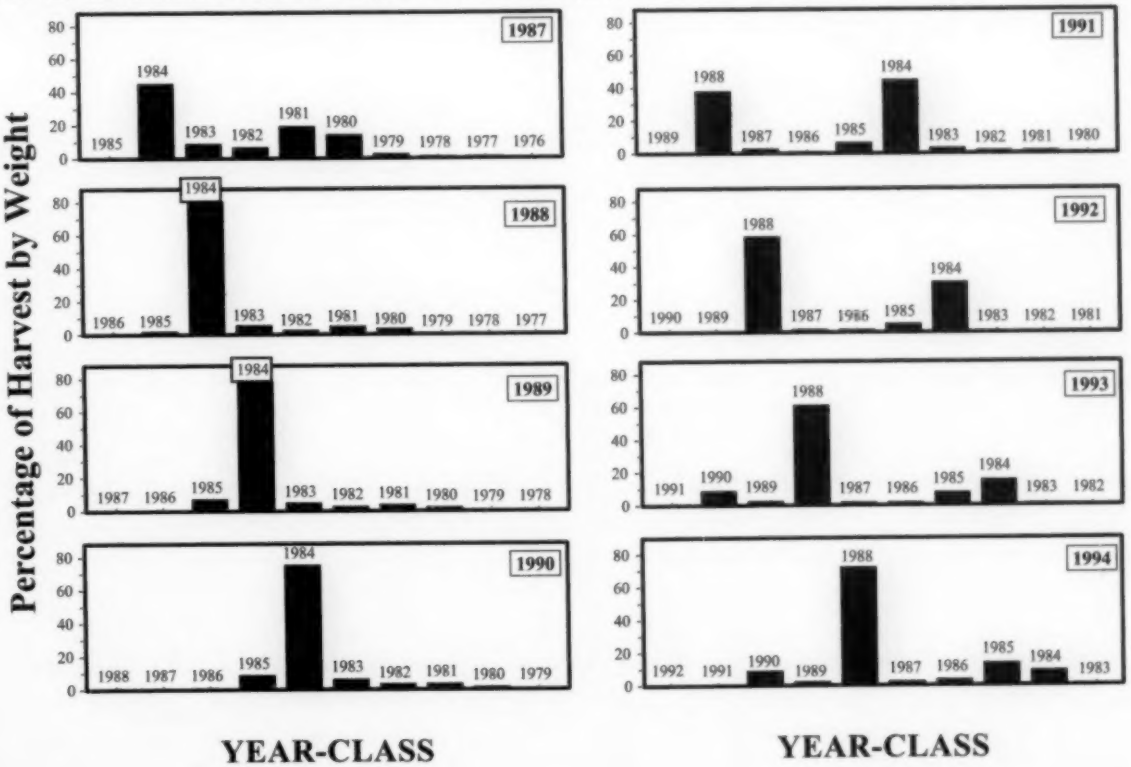

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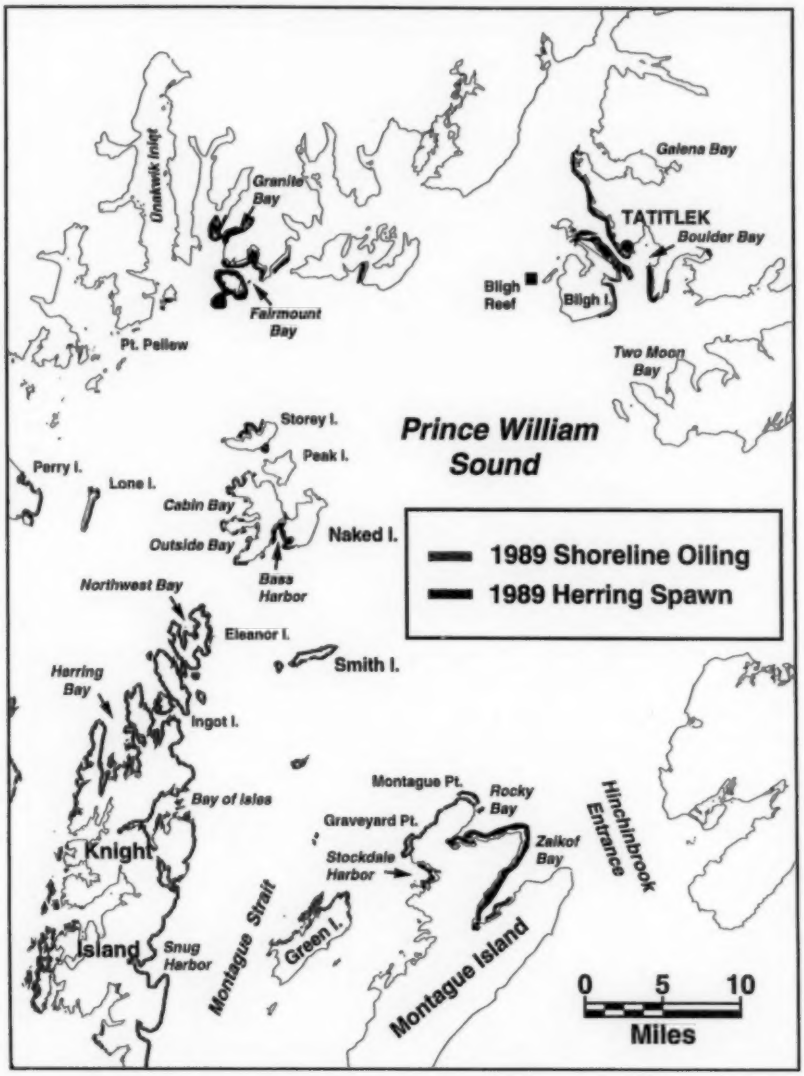
Fig. 4. Map of oiled shoreline and Pacific herring spawn in PWS, Alaska, 1989.



land and Knight Island archipelagos and on Smith, Green, and Latouche islands in Montague Strait (Galt et al. 1991*a*, 1991*b*) (Fig. 4). *Exxon Valdez* oil (EVO) began exiting from the southwest passages of PWS on March 30, and by the second week in April, 20–25% of the spilled oil had moved into the GOA (Galt et al. 1991*b*). Galt et al. (1991*b*) estimated that 35% of the spilled oil evaporated (mostly during the first 2 weeks postspill), 40% affected shorelines within PWS, and 25% passed from PWS into the GOA. Northern facing shorelines on Smith, Eleanor, Ingot, and Knight islands received the heaviest oiling. Green and Latouche islands received smaller amounts of stranded oil. Oil stranding was patchy and light on the shorelines of the Naked Island archipelago and the northern end of Montague Island, all of which were major spawning areas in 1989.

In 1989, ground-based surveys found some degree of oiling along 783.7 km, or about 16%, of the 4830 km of PWS shoreline (Neff et al. 1995). The extent of shoreline oiling fell substantially over the next 3 years to 6.7, 2.0, and 0.2% of the PWS shoreline in 1990, 1991, and 1992, respectively. The extent of heavy oiling decreased from 2.9% of the PWS shoreline in 1989 to 0.003% in 1992.

The EVOS occurred about 2 weeks before the April 14 peak of herring spawning in PWS. Herring move to shallow water before spawning and then spawn in the intertidal and subtidal areas (Hay 1985). In 1989, herring deposited spawn along 158 km of PWS shoreline (Brady et al. 1990), and the timing of the spill raised concern for potential effects to herring. Because of concern for potential oil exposure of herring, the 1989 spring herring fisheries were canceled. Fortunately, over 90% of the spawn length subsequently occurred along shorelines that were not oiled and that were

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well away from the spill-affected areas (Fig. 4) (Pearson et al. 1995). Harvesting was resumed in PWS in fall 1989 and continued without interruption until spring 1993.

Hypotheses

To seek precedents for the various hypotheses that could explain the 1993 PWS herring collapse, we first reviewed the world literature on stock collapses, emphasizing herring (Table 1). Among 46 collapses in herring stocks around the world, overfishing was the most frequently cited cause of stock collapse (74% of the cases). Overfishing as the sole cause was cited in 37% of the cases. In 37% of the cases, overfishing was seen to have acted in combination with such factors as natural changes in the environment (22%), changes in food supply (2%), changes in the environment and in food supply (7%), and density-dependent responses (7%). Environmental change was the second most frequently cited cause (50% of the cases), predominantly in combination with other factors (37%) rather than alone (13%). Changes in food supply were cited in 15% of the cases, always in combination with other factors. Predation was seen in one case (2%) in combination with overfishing and environmental change. Single-factor causes other than overfishing or environmental change were rare. Disease, pollution, and habitat modification constituted one case (2%) each. Oil spills were not cited as a cause in any of the previous herring stock collapses. Our finding of overfishing as the most frequent historical cause of stock collapses is consistent with Hutchings' (1996) hypothesis, based on his analysis and the theoretical analysis of Myers et al. (1995), that fishing mortality rather than nonfishing mortality is the primary cause of fish stock collapses worldwide. Thus, the literature provides historical precedents for the hypotheses discussed in this paper.

An example of how overfishing can produce a stock collapse can be found in the British Columbia herring fisheries of the 1960's (Hourston 1980). Eight of the nine major British Columbia herring stocks sharply declined between 1963 and 1967. Hourston (1980) attributed the declines to three factors: poor recruitment, increased fishing mortality due to substantially increased fishing efficiency, and stock assessment procedures that were not able to detect the downward trend in spawning escapement until it was well advanced. After the fishery closures, 6 years was required for the population levels to return to normal.

In the case in which pollution caused a herring stock decline, Winters et al. (1986) studied the effects of an elemental phosphorus spill that killed 80% of an adult herring stock in Placentia Bay, Canada. The catastrophic mortality did not affect recruitment, and the Placentia Bay stock subsequently recovered within 3 years.

In the case in which an epizootic was concluded to be the cause of a herring stock decline, Tibbo and Graham (1963) had three lines of strong evidence to support their conclusion. First, heavy and widespread mass mortalities and abnormal behavior were directly observed in Atlantic herring (*Clupea harengus*) in the Gulf of St. Lawrence during spring and summer 1954. Second, histopathological examination revealed infections by the fungus *Ichthyosporidium hoferi*, and experimentation confirmed the pathogen's ability to infect, damage, and kill Atlantic herring. Third, an abrupt and substantial decline (30–40%) in herring landings in the herring fishery followed the epizootic. Thus, it is clear that under specific conditions, an epizootic can decrease herring stock levels.

Based on the background literature, the three categories of hypotheses to explain the 1993 decline in the PWS herring population can be listed as follows.

(*i*) Three hypotheses postulate that the 1989 oil spill caused the 1993 decline:
- H1. Acute toxic effects of oil exposure in 1989 caused the 1993 decline.
- H2. Toxic effects of oil lingering in PWS through 1992 or 1993 produced the decline.
  - H2*a*. Lingering oil affected the herring directly.
  - H2*b*. Lingering oil affected the herring indirectly by reducing their food supply.
- H3. Delayed effects of the 1989 oil spill induced a disease that caused the decline.

(*ii*) Two hypotheses postulate that a harvesting effect caused the decline:
- H4. Overfishing led to the decline of the PWS herring stock.
- H5. Underfishing allowed the herring biomass to increase to the point that density-dependent mechanisms led to the decline.

(*iii*) Four hypotheses postulate that a series or combination of natural factors caused the decline.
- H6. Poor nutrition alone or in conjunction with a disease caused by an opportunistic pathogen produced substantially lower herring survival that in turn caused the decline.
  - H6*a*. Recently increasing herring biomass increased intraspecific competition for prey (a density-dependent response.
  - H6*b*. Recently increasing biomass of other fish increased interspecific competition for prey.
  - H6c. Large-scale oceanic processes reduced food supply that in turn lowered the nutritional status of the PWS herring.
- H7. An infectious disease caused the 1993 decline.
  - H7*a*. Disease alone caused the 1993 decline.
  - H7*b*. Low temperatures triggered a disease outbreak that in turn reduced survival.
- H8. Increased predation reduced the population level.
- H9. Natural chaotic population dynamics produced the decline, perhaps by a stochastic process in which small changes in the physical or biological environment produced a large, abrupt change in the PWS herring population.

PWS herring exposure during the EVOS

The issue of exposure of the various herring life stages to oil spill hydrocarbons in the waters of PWS is critical to a test of several of the hypotheses positing spill effects; for this reason, we review herein the data that document the levels of exposure to the spill. Direct measurements of the

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Table 1. Summary of collapses of Atlantic and Pacific herring and other fish stocks.

Stock	Time period	Extent of collapse			Reported causal mechanism	Source(s)
		From	To	Units in millions		
Atlantic herring						
Atlantico-Scandian, Norway	1957–1963	10	2.5	t	Lack of adult recruitment, exploitation of young herring	Jakobsson 1985
Atlantico-Scandian spring-spawning herring	1966–1969	4	0.25	t	Lack of adult recruitment, exploitation of young herring	Jakobsson 1985
Atlantico-Scandian spring-spawning herring	1960–1962	na	na	na	Water temperature anomalies, decreased food abundance	Devold 1963
Atlantico-Scandian spring-spawning herring	1968–1991	na	na	na	(*i*) High fishing pressure, (*ii*) reduced winter food supply altered migration behavior	(*i*) Dragesund and Ulltang 1978; (*ii*) Jakobsson 1992
Icelandic spring-spawning herring	1960–1965	0.7	0.02	t	Increased fishing mortality, change in recruitment	Jakobsson 1985
Icelandic summer-spawning herring	1960–1965	0.32	0.07	t	Increased fishing mortality, change in recruitment	Jakobsson 1985
North Sea	1964–1969	2.5	0.7	t	Exploitation of the 2- to 7-year class, poor recruitment	Jakobsson 1985
North Sea	Mid-1970's	na	na	na	(*i*) Heavy fishing pressure, (*ii*) recruitment failure from larval transport out of area	(*i*) Corten 1986; (*ii*) Corten and Kemp 1992
Northern North Sea	1964–1969	12 000	2000	Fish	Water temperature, alterations in currents, food competition, fishing pressure	Rothschild 1986
Central North Sea	1945–1955	8 000	2000	Fish	Water temperature, alterations in currents, food competition, fishing pressure	Rothschild 1986
Southern North Sea	1945–1955	8 000	2000	Fish	Water temperature, alterations in currents, food competition, fishing pressure	Rothschild 1986
Southern North Sea	1960's	na	na	na	Dam construction blocked route to spawning grounds	Zilstra 1963
West Scotland, Division VIa	1974–1979	0.25	0.05	t	(*i*) Overfishing, (*ii*) alteration in oceanic currents, changes in larval drift and food availability	(*i*) Jakobsson 1985; (*ii*) Corten 1990
Celtic Sea, southern Ireland, Division VIIj	1969–1974	0.1	0.03	t	Overfishing, poor recruitment	Jakobsson 1985
St. Mary's Bay, Nfld.	1968–1969	0.146	0.062	t	Mass mortality from industrial spill of elemental phosphorus	Winters et al. 1986
Fortune Bay, Nfld.	1971–1972	0.343	0.0196	t	Fishing pressures, environmental factors including temperature and salinity	Winters et al. 1985
Chaleur Bay, Gulf of St. Lawrence	1954–1955	na	na	na	Epizootic fungus	Tibbo and Graham 1963
Gulf of Maine	1962–1964	0.259	0.048	t	Overfishing, sea surface temperature (SST) changes	Anthony and Fogarty 1985
Gulf of Maine	1966, 1969, 1974	na	na	na	Correlated with low temperatures	Anthony and Fogarty 1985
Georges Bank	Early 1970's	na	na	na	SST changes, overfishing	Anthony and Waring 1980
Scotian Shelf	1968–1972	5	1.5	t	Overfishing, possibly density-dependent emigration	Sinclair et al. 1985
Scotian Shelf	1974–1978	6	1	t	Overfishing, possibly density-dependent emigration	Sinclair et al. 1985
Gulf of St. Lawrence	1970–1974	1.2	0.5	t	Overfishing, possibly density-dependent emigration	Sinclair et al. 1985

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Table 1 (*continued*).

Stock	Time period	Extent of collapse			Reported causal mechanism	Source(s)
		From	To	Units in millions		
Pacific herring						
Bering Sea	1960–1962	na	na	na	Low salinity indicative of poor mixing, low nutrients, and poor food stocks	Mysak 1986
Bering Sea	1970–1972	1.2	0.2	t	(*i*) Overfishing, lack of recruits, (*ii*) wind-driven transport, SST changes, overfishing, (*iii*) increase in walleye pollock stocks possible cause	(*i*) Fried and Wespestad 1985; (*ii*) Wespestad and Gunderson 1990; (*iii*) Laevastu and Favorite 1980
Sitka Sound	1976–1977	400	100	Fish	Environmental factors implicated	Collie 1990
Sitka Sound	1980–1981	450	200	Fish	Environmental factors implicated	Collie 1990
Sitka Sound	1984–1985	850	150	Fish	Environmental factors implicated	Collie 1990
Sitka Sound	1979–1981	400	100	Fish	SST changes, larval transport, overfishing	Zebdi 1991
Sitka Sound	1983–1985	450	200	Fish	SST changes, larval transport, overfishing	Zebdi 1991
Sitka Sound	1987–1989	850	150	Fish	SST changes, larval transport, overfishing	Zebdi 1991
British Columbia	1967–1968	na	na	Fish	Overfishing	Trumble and Humphreys 1985
Queen Charlotte Islands, B.C.	1965–1967	443	40	Fish	Overfishing, decreased recruitment	Hourston 1980
Northern British Columbia	1965–1968	622	32	Fish	Overfishing, decreased recruitment	Hourston 1980
Upper central British Columbia	1965–1968	463	2	Fish	Overfishing, decreased recruitment	Hourston 1980
Lower central British Columbia	1966–1968	438	36	Fish	Overfishing, decreased recruitment	Hourston 1980
Middle east coast British Columbia	1966–1967	260	70	Fish	Overfishing, decreased recruitment	Hourston 1980
Lower east coast British Columbia	1966–1968	250	78	Fish	Overfishing, decreased recruitment	Hourston 1980
Lower west coast British Columbia	1966–1967	321	58	Fish	Overfishing, decreased recruitment	Hourston 1980
Upper west coast British Columbia	1961–1963	402	60	Fish	Overfishing, decreased recruitment	Hourston 1980
Strait of Georgia, Johnstone Strait	1962–1966	3 500	200	Fish	Correlated with SST and changes in sea level	Stocker et al. 1985
West coast Vancouver Island	1958–1965	2 000	300	Fish	Correlated with SST and salinity	Stocker et al. 1985
Prince Rupert District	1961–1965	2 500	200	Fish	Correlated with SST	Stocker et al. 1985
Strait of Georgia	1961–1963	1 700	500	Fish	Increased fishing efficiency, decreased escapement, possibly linked to SST changes	Ketchen et al. 1983
Strait of Georgia	1956–1958	2 300	500	Fish	Increased fishing efficiency, decreased escapement, possibly linked to SST changes	Ketchen et al. 1983
Hokkaido, Japan	1950's	na	na	na	Overfishing, SST changes, changes in Kuroshio Current	Morita 1985; Gulland 1988

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Table 1 (*concluded*).

Stock	Time period	Extent of collapse			Reported causal mechanism	Source(s)
		From	To	Units in millions		
Other fish						
Peruvian anchovy	1970–1972	18	2	t	(*i*) El Niño and overfishing established as cause, (*ii*) predation of eggs by sardine, possibly density-dependent factors, population pulse noted before collapse	(*i*) Lasker 1985; (*ii*) Gulland 1988
Peruvian sardine	1949–1950	na	na	na	Environmental factors, El Niño possibly	Lasker 1985
California sardine	1945–1960	1	0.003	t	(*i*) Overfishing, changing currents and water temperature, food competition, (*ii*) possibly cannibalism	(*i*) Rothschild 1986; (*ii*) Gulland 1988
California sardine	1948–1950	3 181	102	t	Overfishing, lowered recruitment	Iles 1973
South African sardine	1962–1964	1.8	0.2	t	Overfishing, El Niño	Gulland 1988
North Sea haddock	1963, 1968, 1975	na	na	na	High total stock biomass the previous year	Cook and Armstrong 1986
Georges Bank haddock	Late 1920's, 1967	na	na	na	Overfishing	Grosslien and Hennemuth 1973
Scotian Shelf haddock, Division 4x	1978, 1983	na	na	na	Density-dependent larval emigration	Frank 1992
West Greenland cod	1968–1971	na	na	na	Low water temperature	Gulland 1988
Northern cod	1962–1992	1.6	0.022	t	Overfishing	Hutchings 1996; Myers and Cadigan 1995
Pacific halibut	1960–1970	420	160	t	Overfishing, altered sex ratio, decreased recruitment	Deriso 1986

Note: t = tonnes (metric tons).

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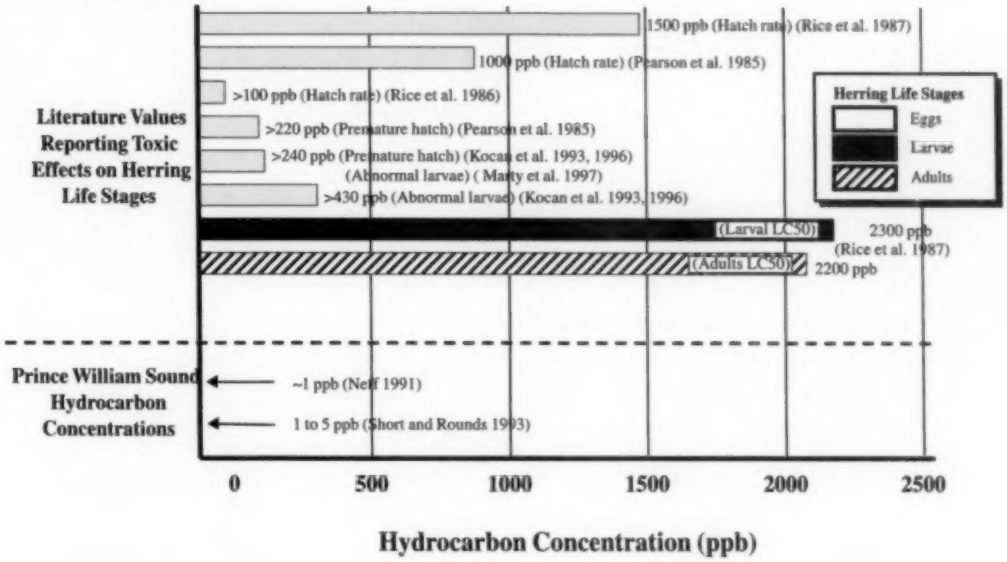
Fig. 5. Literature values reporting toxic effects of petroleum hydrocarbons on Pacific herring compared with hydrocarbon concentrations measured from PWS.


1500 ppb (Hatch rate) (Rice et al. 1987)
1000 ppb (Hatch rate) (Pearson et al. 1985)
>100 ppb (Hatch rate) (Rice et al. 1986)
>220 ppb (Premature hatch) (Pearson et al. 1985)
>240 ppb (Premature hatch) (Kocan et al. 1993, 1996)
(Abnormal larvae) (Marty et al. 1997)
>430 ppb (Abnormal larvae) (Kocan et al. 1993, 1996)
Literature Values Reporting Toxic Effects on Herring Life Stages
Herring Life Stages
Eggs
Larvae
Adults
(Larval LC50)
2300 ppb
(Rice et al. 1987)
(Adults LC50)
2200 ppb
Prince William Sound Hydrocarbon Concentrations
~1 ppb (Neff 1991)
1 to 5 ppb (Short and Rounds 1993)
0
500
1000
1500
2000
2500
Hydrocarbon Concentration (ppb)

actual hydrocarbon concentrations in the water column of PWS were made in two programs during 1989 and 1990. The results of these two programs, as reported by the National Oceanic and Atmospheric Administration (NOAA) (Short and Rounds 1993), Neff (1991), and Neff and Stubblefield (1995), found that water column concentrations of petroleum hydrocarbons in PWS peaked during April 1989 and then fell to background levels by August 1989. The peak in water column concentrations for 35 primary offshore stations within the spill trajectory averaged less than 2 parts per billion (ppb) for volatile aromatic hydrocarbons (VOA's) and about 0.2 ppb for polycyclic aromatic hydrocarbons (PAH's) (Neff 1991; Neff and Stubblefield 1995) (Fig. 5). For 51 nearshore monitoring stations most applicable to our concerns, VOA concentrations in the water column exceeded 5 ppb in less than 2% of the samples from March through October 1989. The highest VOA concentration (16 ppb) was observed in June 1989 for a surface water sample in Northwest Bay, a heavily oiled bay in the Knight Island archipelago. Similarly, a NOAA program (Short and Rounds 1993) sampled seawater at 1, 3, and 5 weeks postspill at 1- and 5-m depths at 30 stations in PWS. They also found the highest PAH's in seawater to be at stations near heavily oiled beaches. PAH concentrations ranged up to 6.6 ppb at Snug Harbor and from 1.9 to 5.2 ppb near other oiled beaches in the Knight Island archipelago and north of Smith Island. Sampling stations at the margins or outside the spill path had seawater PAH concentrations of 0.4–1.5 ppb.

These water column concentrations were also verified using an equilibrium partitioning approach and measured levels of hydrocarbons from tissues of mussels (Neff and Burns 1996). PAH concentrations measured from intertidal mussels sampled from areas where herring spawned ranged from 19 to 2504 ppb (Brown et al. 1994). Tissue burdens for mussels within and outside the oil spill trajectory averaged 753 and 49 ppb, respectively (Brown et al. 1996). Using equilibrium partitioning, these mussel concentrations resulted from and were equivalent to PAH concentrations of less than 1 ppb in nearshore waters (Neff and Burns 1996). Therefore, data from monitoring programs of both water and mussels support the conclusion that water column exposures to oil spill hydrocarbons were very low, in the few parts per billion range.

Assessment of the hypotheses

Below, we examine each hypothesis and the associated information. Where the nature of the hypothesis and the available information allowed, our evaluation focused first on identifying the conditions that would be necessary for this hypothesis to explain the 1993 decline and whether such conditions were present. We also identified the biological effects that would be expected under each hypothesis and assessed whether such effects were evident from the field data.

H1. Acute toxic effects of oil exposure in 1989 caused the 1993 decline

This hypothesis posits that oil exposure during the EVOS in 1989 produced acute toxic effects that caused the 1993 decline. The hypothesis requires that the 1989 exposure to oil be sufficiently high to produce mortality or other acute toxic effects and that the effects be of a nature and magnitude sufficient to produce the decline 4 years later in 1993. Specific effects under this hypothesis include mass mortality of adult herring during the spill and mass mortality of the eggs, larvae, and juvenile herring that would become evident later as a lower than expected recruitment strength.

Although there is no doubt that exposure to crude oil in high concentrations can be toxic to herring, the nature and level of exposure to oil spill hydrocarbons need to be evaluated to determine whether the levels shown to produce acute toxic effects were reached during the spill or in the year af-

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ter the spill. This section reviews the 1989 and 1990 data to assess whether concentrations necessary for acute toxic effects were present.

Because the magnitude of exposure varies substantially with herring life stage, our evaluation is structured accordingly. We discuss the potential exposure routes and the concentrations known to produce acute toxic effects and then compare those concentrations with the environmental concentration of hydrocarbons measured in PWS. We then examine the available information for indications of the biological effects on the herring population expected under this hypothesis.

Potential oil exposure of herring eggs in 1989

Because herring spawn in nearshore areas, they have potential for exposure to oil spill hydrocarbons through exposure of both prespawning adults to oil-contaminated seawater and eggs after they are deposited in the shallow subtidal and intertidal areas. However, laboratory studies have shown that exposure of prespawning adults to even highly contaminated seawater does not produce adverse effects on the eggs. In a laboratory experiment, prespawning adult herring were exposed to the water-accommodated fraction of weathered ANS crude oil with PAH concentrations of 4–60 ppb, and the eggs and hatching larvae showed no increases in mortality or morphological or cytogenetic abnormalities (Carls et al. 1995). The hatching rate of eggs taken from adult herring exposed to the water-soluble fraction of fresh Cook Inlet crude oil was not affected by exposures at 1600 ppb for either 2 or 12 days (Rice et al. 1987). These toxicity tests were done using the water-soluble fraction of crude oils prepared by gently mixing oil and water. The main hydrocarbons present in the water-soluble fraction include the low relative molecular mass PAH's that are responsible for most of the toxicity of crude oil (Rice et al. 1977; Neff and Stubblefield 1995). Thus, the water-soluble fraction used in toxicity tests can be compared with the composition of the hydrocarbon fraction present in the PWS water column following the spill.

Once the eggs are deposited in nearshore areas, they are potentially at risk of exposure to oil washing from adjacent oiled shorelines. However, laboratory studies summarized in Fig. 5 demonstrated that exposure of herring eggs to oil concentrations over 200 ppb in the water column is the threshold for toxic effects. Pearson et al. (1985) found that oil adhering to eggs was the major mechanism for inducing increased levels of larval abnormalities and other effects. In a series of experimental treatments, Pearson et al. (1985) found that water column concentrations up to 4 700 ppb monoaromatic hydrocarbons and 28 000 ppb total hydrocarbons do not produce substantially higher frequencies of abnormal larvae, unless oil visibly adheres to the eggs. Hay et al. (1995) found in laboratory experiments with Pacific herring that direct deposition of eggs on natural spawning substrate oiled during a spill induced egg mortality, larval mortality, and morphological abnormalities.

The significance of these laboratory exposure studies to the PWS herring population can be determined by comparing known-effect concentrations from these laboratory studies with the hydrocarbon exposures actually measured in PWS during the EVOS (Fig. 5). Immediately after the spill, the peak concentrations of petroleum hydrocarbons in the water column were about 200–1000 times lower than those toxic to herring eggs, and concentrations subsequently dropped to trace background levels. Thus, the observed levels of oil concentrations in the water column do not support the position that peak oil exposure in 1989 was sufficient to produce mass mortality or other toxic effects in the deposited herring eggs.

Spawning distribution and exposure

Because herring spawn along shorelines, there was initial concern over the exposure of spawn to oiling conditions along intertidal and subtidal habitats. Total spawn length was above average in 1989, but the overlap between oiled shorelines and herring spawn proved to be low. The total length of spawn in 1989 was 158 km, the second highest total spawn length in PWS since observations began in the early 1970's (Donaldson et al. 1993). Pearson et al. (1995) estimated as a worst case that between 9 and 10% of the total beach length of 1989 PWS herring spawn was along oiled shorelines and that most of this was along those classified by NOAA as lightly oiled, with only 1% of the spawn along those moderately to heavily oiled (i.e., the northern end of the Knight Island archipelago) (Fig. 4; Table 2). A similar analysis by the interagency *Exxon Valdez* Oil Spill Trustee Council estimated that 5–10% of the spawning grounds were oiled in 1989 (McCammon and Evans 1994) (Table 2).

In addition to the low spatial overlap between beach oiling and spawn in 1989, the temporal overlap between the observed presence of slicks and the herring spawning along oiled beaches was small. Detailed examination of spill trajectory observations reveals that the oil slick had passed by the spawning areas (Knight, Naked, and Montague islands) and oil stranding had occurred about 9–12 days before spawning commenced. Scattered sheens, not slicks, were present during spawning and incubation in 1989.

Based on diver transects for egg deposition and PAH concentrations in mussels taken from bays sampled for eggs on kelp, Brown et al. (1994) estimated that between 40 and 50% of the eggs were potentially exposed to EVO in 1989. In a revised estimate based on herring spawn within the oil trajectory, Brown et al. (1996) estimated that the spawn length exposed to oil was 35–43% of total spawn, and the eggs exposed to oil were 41–52% of the total eggs deposited in PWS (Table 2). However, back-calculation from the PAH body burdens in mussels indicates that the water PAH concentrations were less than 1 ppb (Neff and Burns 1996), two orders of magnitude lower than concentrations known to be toxic to eggs. An estimate of exposure that includes all the eggs within the oil trajectory includes exposures that were essentially negligible, such as those in the subtidal areas of oiled beaches. Thus, an exposure estimate of 40–50% of PWS herring eggs in 1989 is clearly an overestimate.

Recent findings by Marty et al. (1997) suggest an exposure of herring eggs somewhat greater than about 10% but still not approaching 40–50%. Histopathological lesions in herring larvae can be used to indicate exposure of the eggs. In field-collected larvae earlier examined by Marty et al.

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Table 2. Estimates of extent of exposure of Pacific herring eggs following the EVOS, 1989.

Basis of estimate	% of total PWS spawn length	% of total PWS eggs	Source(s)
Assuming all eggs within oil trajectory were exposed			
Including Zaikof Bay	43.3	52.0	Brown et al. 1996
Excluding Zaikof Bay	34.6	41.0	Brown et al. 1996
Assuming all intertidal eggs within the oil trajectory were exposed			
Including Zaikof Bay	—	16.6	Our calculation from above numbers and using 32% of eggs in the intertidal average for oiled areas from McGurk and Brown 1996
Excluding Zaikof Bay	—	13.1	
Assuming all eggs along oiled shorelines were exposed	1–10	—	Pearson et al. 1995
	5–10	—	McCammon and Evans 1994
All nearshore larvae with ascites hatched from oil-exposed eggs			
Assuming 100% hatching rate	—	17	Marty et al. 1997
Assuming 70% hatching rate	—	24	Our calculation from data above
Assuming observed rate of direct oiling of eggs-on-kelp samples applies to entire PWS	—	4	Pearson et al. 1995
Assuming all eggs in bays with PAH concentrations above 100 ppb in eggs-on-kelp samples were exposed	6	—	Cabin Bay, Outside Bay, and Montague Point to Graveyard Point; Pearson et al. 1995

(1993*a*, 1993*b*), no histopathological lesions were found. However, in examining larvae collected from the nearshore in 1989 by McGurk and Brown (1996), Marty et al. (1997) found histopathological lesions (ascites and pericardial edema) that match lesions found in larvae hatching from eggs exposed to EVO in the laboratory by Kocan et al. (1996). Pericardial edema has previously been found in herring larvae hatching from eggs exposed to oil in the laboratory (Linden 1978; Smith and Cameron 1979; Pearson et al. 1985). Marty et al. (1997) found that ascites occurred in 16% of the larvae from two oiled areas and in 1% of the larvae from two unoiled areas in PWS. In the larvae from a laboratory experiment of Kocan et al. (1996), ascites occurred at 10% in controls and the 100-ppb (micrograms per litre) treatment, at 60% in the 240- and 480-ppb treatments, and at 100% in the 2400-ppb treatment. All treatment levels in this laboratory experiment were substantially higher than the peak PWS water column concentrations discussed above and reported in Neff (1991), Short and Rounds (1993), and Neff and Stubblefield (1995). Although Marty et al. (1997) argued by analogy with experimental exposures of salmon eggs to oil that low water column levels below 1 ppb over the whole incubation period could give rise to the observed rate of ascites, we suggest that direct coating of herring eggs by oil is still the most likely mechanism for induction of these lesions. Marty et al. (1997) found that all larvae with ascites also had pericardial edema. Pearson et al. (1985) found elevated frequencies of pericardial edema in oil treatments with 4.4 ppb in the water column but in which oil droplets adhered to the eggs. Treatments with oil levels up to 2800 ppb total hydrocarbons did not substantially increase larval abnormalities when oil droplets were not visibly adhering to eggs (Pearson et al. 1985). The ascites frequency of 16% reported by Marty et al. (1997) for two oiled PWS bays then argues that the frequency of such direct coating by oil may have been greater than the 10% worst-case estimates posited by Pearson et al. (1995) and McCammon and Evans (1994).

In summary, there were no observations of widespread, substantial EVO exposure of PWS herring eggs in 1989. Estimates of exposure ranged from 4 to 50% of the total number of eggs in PWS (Table 2). Observations of direct contact between oil and herring were localized and represented less than 10% of the total spawn length in PWS during 1989. The recent findings of Marty et al. (1997) suggest exposure of eggs to be 15–25% and to be at low levels. Because of the low overlap in space and time between the distribution of nearshore and beached oil and the distribution of herring spawning, there was no widespread coating of the eggs with oil droplets, the condition most likely to produce effects in the eggs.

Potential oil exposure of larvae, juveniles, and adults in 1989

If the egg stage was not exposed to acutely toxic levels of oil, proof of Hypothesis H1 requires that one or all of the remaining life stages be exposed to toxic oil concentrations. Of the three possible routes by which PWS herring were exposed to EVO, i.e., via oil-contaminated seawater, via ingestion of oil droplets or oil-contaminated prey, and via direct contact with oil slicks and sheens, the exposure route of primary concern for larval, juvenile, and adult herring is via the water column. Laboratory studies reviewed by Pearson et al. (1995) have shown that exposures to seawater contaminated with oil above 1000 ppb for a period of 1 to several days are needed to produce mortality in adult and larval herring.

During the EVOS, concentrations of petroleum hydrocarbons in the water column averaged about 1000 times lower than those shown to be toxic to adult and larval herring in laboratory studies: water column concentrations of petro-

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leum hydrocarbons in PWS peaked at a few parts per billion during April 1989 and then fell to background levels of 0.4–1.5 ppb by August 1989 (Neff 1991; Short and Rounds 1993; Neff and Stubblefield 1995).

PAH tissue burdens measured directly in adult PWS herring also do not suggest substantial water column exposure to EVO in 1989. Tissue burdens in adult herring collected by ADFG in PWS in 1989 were below the method detection limits (20–40 ppb for individual analytes) (Brown et al. 1994). In late April and early May 1989, Bienert et al. (1991) collected 62 herring from two sites in PWS. Total PAH's in gonadal tissue ranged from not detected to 36 ppb in Galena Bay (unoiled) and from not detected to 64 ppb in Rocky Bay (lightly oiled) (method detection limits 1–4 ppb for individual analytes). For comparison, 1994 laboratory experiments exposing adult prespawning herring to the water-accommodated fraction of ANS crude oil from 2 to 40 ppb for 8 days showed PAH accumulations in herring that varied from about 80 to 8000 ppb (Carls et al. 1995). A comparison of these laboratory accumulations with those observed in PWS in 1989 suggests that herring collected by Bienert et al. (1991) in 1989 were exposed to concentrations of less than 2 ppb.

A second potential route for exposure for adult, juvenile, and larval herring is through ingestion of oil droplets or oil-contaminated prey. Although no direct observations of ingested oil in adult, juvenile, or larval herring exist for 1989, Brown et al. (1994) postulated that because copepods, a major prey item of larval, juvenile, and adult herring, may ingest oil droplets (Conover 1971), exposure of herring by ingestion could be an important route. However, Capuzzo's (1987) review concluded that uptake of petroleum hydrocarbons by ingestion of oil or oil-contaminated prey is quite small for fish. Poor uptake of hydrocarbons via ingestion occurs because only a small portion of the PAH's in oiled food passes the gut wall of fish (Van Veld et al. 1988; Varanasi et al. 1989; Lemaire et al. 1992). Further, prespawning and spawning herring do not feed (Carlson 1980); therefore, adult exposure by ingestion could not have begun in PWS until mid-April or May.

The third potential route of exposure is by direct contact with oil slicks and sheens. In the absence of specific observations of herring at the surface during the spill and of other supporting data, an assessment of this route is inferred from the behavioral patterns of herring and the presence of slicks and sheens in PWS. Exposure of herring to slicks and sheens would be intermittent because adult and juvenile herring migrate vertically to feed in the upper water column at dawn and dusk but remain in deeper waters during the day to avoid predators. Carlson (1980) found that from late May to September, Pacific herring schools were constantly moving and feeding. Although the schools moved from the surface to near bottom, most schools concentrated at depths of 5–37 m, where zooplankton were abundant.

Aerial surveys of oil sheens originating from shorelines affected by the EVOS from September 1989 to September 1990, conducted by Taft et al. (1995), identified 827 nonbiogenic sheens. The numbers and volumes of these sheens dropped dramatically after the 1989–1990 winter storms; EVO sheens were not effectively present beyond spring 1990 (Taft et al. 1995).

Fluorescent aromatic hydrocarbons (FAC's) in fish bile were also studied as a potential indicator of hydrocarbon exposure, and Brown et al. (1994) reported elevated levels of FAC's in the bile of adult herring collected near heavily oiled beaches in the Knight Island archipelago in summer 1989 and from an unoiled area, Port Chambers on Montague Island, in spring 1990. Although the use of FAC's as an indicator of recent hydrocarbon exposure is gaining general acceptance (Varanasi et al. 1993), the relationship between the FAC values and the original hydrocarbon source or exposure concentration is not known for most fish, including herring. Further, the FAC data of Brown et al. (1994) are uncorrected for biliary protein, a correction necessary to account for the influence of feeding status on the biliary FAC levels (Varanasi et al. 1993). Consequently, assessing the extent or biological implications of exposure from these FAC data is not possible.

Histopathological observations have also been used as indicators of contaminant exposure and stress, although it is recognized that they can be confounded by numerous natural factors (Overstreet 1988). The histopathological observations in PWS during 1989 do not provide evidence of substantial exposure of adult herring. Marty et al. (1993*a*, 1993*b*) and Bienert et al. (1991) conducted separate histopathological examinations of adult herring collected in PWS in April and May 1989. These studies offer an independent check on the exposure assessments described above. Marty et al. (1993*a*) reported that principal components analysis of 20 histopathological indicators was unable to distinguish between fish from unoiled versus oiled areas. Bienert et al. (1991) found no histopathological indications of exposure in 1989 in 30 fish from one unoiled area, Galena Bay, or in 32 fish from an oiled area, Rocky Bay.

Field-collected herring larvae examined by Marty et al. (1993*a*, 1993*b*) also showed no histopathology. Whereas 16% of field-collected larvae examined by Marty et al. (1997) exhibited lesions matching those found in laboratory-exposed herring eggs, these types of lesions are induced during egg incubation, not during the larval stage. These lesions therefore imply exposure of eggs rather than larvae, as was discussed previously.

Thus, available data indicate that exposure of larval, juvenile, and adult herring during 1989 was minimal. The directly measured hydrocarbon concentrations in the water column were a few parts per billion. The histopathological studies also do not provide evidence of exposure of these life stages. Although some minimal level of exposure cannot be discounted, the demonstrated levels do not approach those likely to induce acute toxic effects in the PWS herring population.

Biological effects of the 1989 oil spill

In order to accept Hypothesis H1, which posits a major acute effect of the spill in 1989, field data from PWS would have to confirm a major mortality or major effect on a sensitive life stage of herring. In this section, we review the extensive field studies that were conducted in 1989 and 1990 in search of such an effect. The potential effects of the EVOS on fish that were adults and juveniles at the time of the spill have been inferred primarily from examination of

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the age structure and population levels in PWS herring, with supporting evidence from histopathological examinations and chemical analyses.

Effects on eggs and larvae: In herring eggs from PWS incubated in the laboratory, Pearson et al. (1995) examined 10 biological response variables, including egg development, hatch, larval survival, larval abnormality rate, larval length, and larval yolk sac volume. In 1989, one response, frequency of developed eggs, was related to the PAH concentrations in the eggs on kelp sampled from the intertidal zone of Cabin Bay. In these eggs, tarry deposits were observed, and presence of EVO was analytically confirmed. Cabin Bay had less than 2% of the total spawn length in PWS during 1989. Brown et al. (1994) found no evidence of an effect of PAH contamination on the in situ mortality of PWS herring eggs in 1989 or in subsequent years. Also, in herring eggs collected in PWS and incubated in the laboratory in 1989, Brown et al. (1994) and Hose et al. (1996) observed morphological abnormalities and cytogenetic abnormalities (rate of anaphase aberrations) in the hatching larvae. They also found that these abnormality rates were significantly higher at two oiled sites, Naked Island and Rocky Bay, than at an unoiled site, Fairmount Bay, in 1989.

During 1989, two series of larval herring collections occurred. In the first, McGurk et al. (1990*a*, 1990*b*) collected nearshore herring larvae with bongo nets in May and June 1989 from two oiled and two unoiled areas. Collections were less than 1 km from spawning areas sampled for egg density. McGurk and Brown (1996) and Marty et al. (1997) analyzed data and larvae from the first collection series. In the second collection series, Norcross and Frandsen (1993) collected herring larvae from offshore areas with Tucker trawls in May, June, and July 1989 at 13, 24, and 44 offshore stations, respectively. Norcross et al. (1994, 1996) analyzed data and larvae from the second collection series.

Analysis by McGurk and Brown (1996) showed peak nearshore abundance in May and early June, with a substantial decline in mid-June. Offshore sampling found low abundance in May, peak abundance in June, and the lowest abundance in July (Norcross et al. 1996). These abundance patterns are consistent with the understanding that herring larvae are abundant in the nearshore in May, just after hatching, and by June are lost to observation in the nearshore through dispersal and growth. Abundance at offshore stations increases in June as herring larvae disperse from the nearshore, and it decreases in July when the larvae grow large enough to avoid capture by sampling nets.

Net avoidance by larger herring larvae can be substantial (McGurk 1992*a*). The nets used by McGurk and Brown (1996) in later cruises and by Norcross et al. (1996) in all 1989 cruises had a mesh width of 0.505 mm and were towed at 1.0 m/s. For such a mesh width and tow speed, the empirical equation of McGurk (1992*a*) indicates that capture rates for herring larvae are 93% for 9-mm larvae and decreases exponentially for larvae longer than 10 mm. The estimated capture rates for 15- and 20-mm larvae are 33 and 13%, respectively (McGurk 1992*a*). McGurk and Brown (1996) and Norcross et al. (1996) did not adjust larval densities or other data for net avoidance.

For nearshore larvae, McGurk and Brown (1996) found no significant differences between oiled and unoiled areas in larval densities, loss rates, or growth rates. The difference in mean larval size (10.9 mm for unoiled areas versus 10.1 mm for oiled areas) was confounded by temperature differences and was judged by McGurk and Brown (1996) to be too slight to offer evidence of an oiled effect. Egg to larvae stage mortality was significantly different between oiled (0.446/day) and unoiled (0.186/day) areas but was confounded by site differences in egg desiccation, predation, and wave scouring such that McGurk and Brown (1996) could not offer the difference as evidence of an oil effect. They noted that the growth rates at all PWS areas (0.10–0.17 mm/day) were about half the growth rate (0.21–0.41 mm/day) for other wild populations of Pacific herring. The occurrence of a second cohort of herring larvae without yolk sacs in the length–frequency distributions at three of the four areas in June 1989 led McGurk and Brown (1996) to suggest that both a fast-growing and a slow-growing cohort emerged in 1989 within PWS.

From the early May 1989 collections of nearshore herring larvae by McGurk et al. (1990*a*, 1990*b*), Marty et al. (1997) found significant differences between oiled and unoiled sites in histopathological lesions (16 versus 1% ascites), cytogenetic abnormalities (35–84 versus 32–40%), and yolk sac scores (about 2.6 versus 0.75). Nearshore larvae examined by Marty et al. (1997) were shorter at oiled sites (about 8.5 versus 9.1 mm) and grew more slowly (0.07–0.10 versus 0.15–0.18 mm/day) than larvae from unoiled sites. The growth rates observed by Marty et al. (1997) were for a shorter time period of 9 days than those observed over 45–50 days by McGurk and Brown (1996). Marty et al. (1997) argued that the pattern of their observations suggests delayed development and growth in the field-collected nearshore larvae. This pattern in the field-collected larvae differed from that found in larvae from eggs exposed in the laboratory by Kocan et al. (1996). Although ascites and pericardial edema were found in both field-collected larvae and larvae from the laboratory exposure experiment, the pattern of lesions and yolk sac reserves in the laboratory larvae was judged by Marty et al. (1997) to be more consistent with premature hatch. Premature hatch and pericardial edema were observed previously in laboratory oiled exposures of herring larvae (Pearson et al. 1985).

For the offshore larvae, Norcross et al. (1996) found elevated larval abnormalities within the spill trajectory for each month of sampling but did not find significant differences between oiled and unoiled areas over the entire 1989 sampling period. The PWS circulation apparently mixed the larvae from oiled and unoiled areas in such a way as to make it "impossible" to discern the origin of larvae collected offshore (Norcross et al. 1996). Over all PWS offshore stations, the graded severity index scores indicated larval morphological abnormality rates of 97, 56, and 78% in May, June, and July 1989, respectively. Norcross et al. (1996) also collected PWS herring larvae in May 1995, and the graded severity index scores indicated a morphological abnormality rate of 77%. For comparison, Purcell et al. (1990) found that the frequency of abnormal herring larvae averaged 24% and ranged to 68% in net samples from a British Columbia bay

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in the absence of any oil exposure. Purcell et al. (1990) attributed the observed larval abnormalities to thermal shock and other stressors acting on incubating eggs exposed to the sun and warm air during unusually low midday tides. Norcross et al. (1996) also found growth rates in offshore larvae of 0.15 mm/day, consistent with those of 0.10–0.17 mm/day found by McGurk and Brown (1996) for the nearshore larvae. Norcross et al. (1996) found that abnormal offshore larvae are shorter than normal offshore larvae.

Altogether, the studies of McGurk (1992*b*), McGurk and Brown (1996), Norcross et al. (1996), and Marty et al. (1997) suggest the following synthesis: the emergence of a second, slower growing cohort in the length–frequency distributions of McGurk and Brown (1996). Further, McGurk and Brown (1996) suggested that the slow-growing nearshore cohort is the one likely to have predominated in the offshore samples of Norcross et al. (1996), due to the timing of the offshore sampling in relation to larval dispersal and the substantial net avoidance of the fast-growing cohort. Applying the net avoidance equation of McGurk (1992*a*) to the average hatch date of May 6 and hatch size of 8.8 mm in McGurk and Brown (1996) and the average growth rate of 0.31 mm/day from McGurk and Brown (1996) for other wild herring larvae populations results in catch rates of 33% by May 26 and 13% by June 12. Larvae growing at 0.15 mm/day would not have catch rates of 33 and 13% until June 17 and July 17, respectively. Differential net avoidance calls into question the larval abnormality rates of Norcross et al. (1996) for 1989 and 1995 and of Purcell et al. (1990) as representative of the true rates of abnormalities in the larval herring populations. These rates are biased upwards and become increasingly so as time goes on and the faster growing normal larvae exponentially increase in their ability to avoid capture.

This synthesis suggests that the early May nearshore samples of McGurk and Brown (1996) examined by Marty et al. (1997) present the best opportunity presently available to discern oil effects on PWS herring larvae. If so, then the findings of Marty et al. (1997) indicate that a syndrome of delayed development and growth was induced during the egg stage and affected about 20% of the PWS larvae. More laboratory experiments in which herring eggs exposed to environmentally realistic levels of oil and to direct coating by oil exhibit the delayed development syndrome are needed before the effects observed by Marty et al. (1997) can be conclusively attributed to oil.

Further observations indicated that oil-related effects on PWS herring eggs were confined to 1989. In 1990, Pearson et al. (1995) found no evidence of direct oiling of herring eggs and no statistically significant relationship between PAH concentrations in eggs on kelp samples and seven biological response variables. In a 1990 laboratory study, McGurk et al. (1991*a*, 1991*b*) incubated eggs to hatch from Fairmount Bay (unoiled), Naked Island (oiled), and Rocky Bay (oiled) in PWS and also Sitka Sound (outside the spill area). The frequency of viable larvae did not vary with area or transect but did vary with depth and interaction of depth and area. McGurk et al. (1991*a*, 1991*b*) concluded that their findings did not support oiling effects on PWS herring eggs in 1990. Brown et al. (1994) and Hose et al. (1996) found no evidence of effects on morphological or cytogenetic abnormality indices in 1990 and 1991. As in 1989, herring larvae from eggs hatched in the laboratory in 1990 showed no histopathological lesions (Marty et al. 1993*a*).

In summary, the bulk of these data do no provide observations of widespread, substantial effects of the EVOS on the 1989 herring eggs or larvae. There was no widespread coating of the eggs with oil and no evidence of increased or mass mortalities of eggs. Pearson et al. (1995) reported only localized effects where the eggs had direct contact with EVO, and such effects were associated with less than 2% of the total spawn length in PWS. Similarly, McGurk (1992*b*) concluded that despite the initial concerns, water column exposure of herring eggs and larvae in PWS to hydrocarbons was not sufficiently high to affect their survival. The recent work of McGurk and Brown (1996), Norcross et al. (1996), and Marty et al. (1997) suggests that potentially about 20% of the PWS herring larvae suffered from a syndrome of delayed development and growth induced during the egg stage. Attributing the syndrome to oil exposure requres more laboratory experiments that specifically demonstrate the syndrome under conditions likely to have occurred during the EVOS.

Effects on juveniles and adults: To accept Hypothesis H1, direct toxic effects on herring juveniles or adults from the 1989 oil exposure would be necessary; however, no mass mortalities occurred in 1989 (Brown et al. 1994). Similarly, the histopathological data provide no evidence of a strong acutely toxic effect. The histopathological analysis of Bienert et al. (1991) included five quantitative histological measurements, for which Haensly et al. (1982) found changes following the *Amoco Cadiz* oil spill. None of these indicators revealed toxic effects in the 1989 EVOS herring samples examined by Bienert et al. (1991).

Furthermore, to accept Hypothesis H1, some population-level effect also would be necessary; however, analysis of events following the spill (1990–1992) does not provide evidence of a population-level effect on PWS herring from the EVOS. The 1984 year-class dominated the fishery before, during, and after 1989 (Fig. 3) and supported record harvests in 1991 and 1992 (Fig. 2). The 1988 year-class, which was 1 year old during the spill, subsequently dominated the fishery and was the major component of the record PWS harvest in 1992 (Fig. 3). The spawning biomass was as predicted in 1990, 1991, and 1992, indicating that there was no abnormal mortality in the adult herring in the 3 years after the spill (Table 3). Pearson et al. (1995) concluded that there is no evidence of large-scale effects on the level of spawning biomass because the 1984 year-class remained strong, a strong 1988 year-class had developed as expected, and postspill harvests had set records. Similarly, using an ASA model, Brown et al. (1994) found that PWS herring biomass reached record levels in 1989 and 1990 and concluded that EVO exposure in 1989 and 1990 was not sufficient to produce population-level effects.

The 1989 year-class, which followed a dominant year-class, was not expected to represent more than a small percentage (1–3%) of the age-class distribution in the PWS seine fishery (Fig. 6) and, accordingly, a small percentage of the PWS biomass. Therefore, even a hypothetical loss of the entire 1989 year-class could not explain the 1993 decline. Even if the localized effect on the herring eggs observed in

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Table 3. Predicted and observed Pacific herring biomasses in PWS, 1988–1993.

	PWS spawning biomass		
Year	Predicted	Observed	Source(s)
1988	42 500	34 270[a]	Brady 1988; Funk 1991
1989	54 899	56 915[a]	Brannian 1989; Funk 1991
1990	56 891	114 998[b]	Funk 1991
1991	96 666	117 143[b]	Funk 1991; Funk and Harris 1992
1992	121 342	128 263[b]	Funk and Harris 1992; Funk 1993
1993	134 133	30 000[c]	Funk 1993, 1994

[a]Estimated peak aerial biomass.
[b]Estimated from egg deposition surveys.
[c]Estimated from aerial surveys.

1989 affected the entire PWS spawning, which it did not, such an effect would not have produced the 1993 decline.

In summary, an extensive test of the data in support of Hypothesis H1 forces us to reject the hypothesis that the 1993 decline was caused by acute toxic effects of oil exposure in 1989. Water column concentrations were insufficient to induce acute toxic effects, and such effects were not evident. Where eggs were coated with oil, decreased egg development was observed, but these cases represented at most a small percentage of the spawn length, and this minor effect on the eggs of the 1989 year-class did not translate into a change at the population level.

H2. Toxic effects of oil lingering in PWS through 1993 produced the decline

Hypothesis H2 posits that oil lingering in PWS through 1993 produced toxic effects that in turn caused the 1993 decline. To evaluate the reasonableness of such a hypothesis, we need to assess the potential for herring exposure to EVOS petroleum hydrocarbons in the postspill years and the sufficiency of such exposure to produce biological effects. The two variations on Hypothesis H2 concern potential for the direct and indirect effects. Because both direct (Hypothesis H2*a*) and indirect effects (Hypothesis H2*b*) would have to be caused by oil concentrations in the water column in post-1989 years, we assess the potential for exposure to oil spill hydrocarbons after 1989 before discussing the two variations of Hypothesis H2.

Exposure after 1989

The water column measurements of hydrocarbons taken by NOAA (Short and Rounds 1993) and by Neff and Stubblefield (1995) each led to the conclusion that hydrocarbon levels were insufficient to cause toxic effects on herring or other fish species even during the spill year, 1989. All available samples taken in late 1989 and early 1990 also confirmed the very low levels of hydrocarbons, which were at trace background levels. Concerns over waterborne exposures were sufficiently low in early 1990 that further water sampling was deemed unnecessary by all parties.

Evidence of EVO's lingering in PWS beyond 1990 or 1991 comes from studies of selected mussel beds beneath which oil was trapped. In 1992, NOAA personnel sampled sediment and mussels from 64 mussel beds in PWS and confirmed with gas chromatography/mass spectrometry that the oil underlying the beds was consistent with moderately weathered EVO (Babcock et al. 1994). Most of the oiled mussel beds are in the Knight Island archipelago and are not in or near herring spawning areas (Fig. 4). The single area sampled by Babcock et al. (1994) that has received herring spawning (Green Island, which received minor herring spawning in 1990) had a relatively low mean sediment total petroleum hydrocarbon concentration of 46 parts per million wet weight.

Babcock et al. (1994) did not measure water column concentrations near the beds, and no water column measures of hydrocarbons were reported after 1992. Water column concentrations back-calculated from the PAH concentrations observed in mussels in 1991 and 1993 by Neff and Burns (1996) showed that the water column concentrations from which the mussels were drawing their burdens were less than 1 ppb, considerably lower than concentrations known to affect sensitive life stages of herring.

To further assess exposure, we also examined fish tissue burdens and biomarkers. FAC's in the bile of fish collected from subtidal areas of oiled and unoiled bays were examined by Collier et al. (1993). They concluded that the FAC levels indicated that subtidal fish in oiled bays had substantially reduced oil exposure in 1990 compared with 1989 and that the exposure was further reduced in 1991.

PAH tissue burdens measured directly in adult PWS herring also do not suggest water column exposure above background in 1989 or 1993. The PAH concentrations measured in adult herring by Brown et al. (1994) and Bienert et al. (1991) in 1989 were given above. The histopathological findings for 1989 discussed above also did not suggest meaningful exposure in 1989, and for the years after 1989, the findings of all investigators do not suggest meaningful exposure beyond 1990. For the fall 1990 herring, Marty et al. (1992) found increased prevalence of macrophage aggregates in liver, spleen, and kidney tissues from oiled areas compared with those from unoiled areas. Marty et al. (1993*a*) found no histological evidence of oil exposure in spring 1991 herring samples. Macrophage aggregates can indicate chemical intoxification but can also derive from other causes such as infectious agents, starvation, and thermal stress, and they are known to increase in concentration with age (Wolke 1992).

Bienert et al. (1991), Elston and Pearson (1993), and Elston et al. (1997) found no hepatic necrosis or other lesions indicating chemical intoxification in 1989, 1993, or 1994. The histopathological analysis of Elston and Pearson (1993) and Elston et al. (1997) included the same five relevant, quantitative histological measurements as were used by Bienert et al. (1991), as described above. Regression analysis of the 1993 data of Elston and Pearson (1993) revealed no statistically significant relationship between the PAH concentrations in the liver of PWS herring and the prevalence of fin erosion, body lesions, liver melanomacrophage index, which quantifies macrophage aggregates, hepatocellular vacuolation index, condition factor (condition factor = weight/length^3), or weight-at-age.

H2a. Lingering oil affected the herring directly

Because there is no strong evidence of substantial or widespread EVO exposure of herring adults during the spill, and no chemical body burden or histopathological evidence of

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Fig. 6. Projected percentage of the seine fishery represented by the 1989 Pacific herring year-class in PWS, 1991–1994.

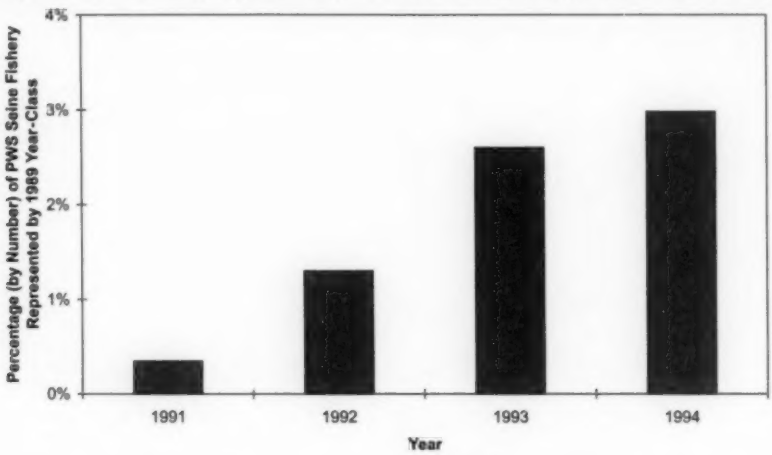
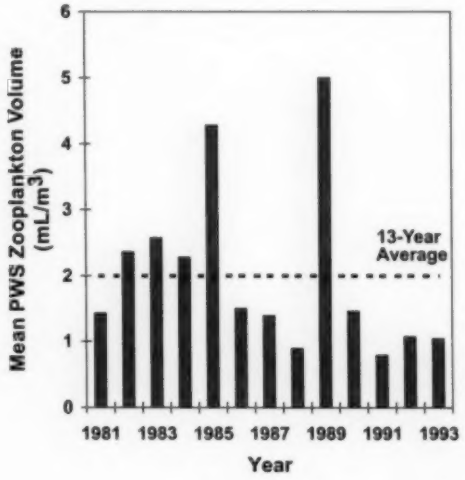


Fig. 7. Potential food supply for Pacific herring in PWS, 1981–1993.



EVO exposure in herring after 1989–1990, direct toxic effects from lingering oil, as posed by Hypothesis H2*a*, are unlikely. The hydrocarbon levels in the PWS water column returned to background in late 1989 at levels several orders of magnitude below those known to cause mortality. We do not find support for the hypothesis that lingering oil in 1992–1993 caused any substantial mortality rates in PWS herring.

H2b. Lingering oil affected the herring indirectly by reducing their food supply

Herring feed in the water column on zooplankton, especially copepods, and the available field data for the abundance of zooplankton, including copepods, show that the PWS herring food supply in the spring of 1989 was the highest on record (Fig. 7) (data from J. Olsen, PWS Aquaculture Corp., Cordova, Alaska). The potential water column exposure, even during the spill, was insufficient to produce mortality in copepods. The LC_{50} for oil-in-water dispersions of crude oil is 13 500 – 73 000 ppb for copepods (Capuzzo 1987), over 1000 times greater than the peak water concentrations measured in PWS during the spill. Moreover, Conover (1971) reported no effect on copepods that ingested droplets of Bunker C oil in the *Arrow* oil spill in Nova Scotia. Studies of other oil spills indicate that zooplankton populations can be reduced during the high exposures during a spill but recover rapidly, and the temporary effects are rarely evident over large areas (National Academy of Sciences 1985). This high level of zooplankton in the year of highest potential exposure is strong evidence against the hypothesis that lingering oil reduced the herring food supply.

H3. Delayed effects of the 1989 oil spill caused the decline

To assess the hypothesis that the 1993 decline in PWS herring was a delayed effect of the EVOS, we need to examine the potential mechanisms that would have exposed the herring to oil spill hydrocarbons in 1989 and could have led to a delayed mass mortality in 1993. Because a viral disease was found among the 1993 herring, one mechanism for the delayed effect suggested by Brown et al. (1994) was that oil exposure in 1989 suppressed the immune systems of exposed herring, leading to a VHSV outbreak 4 years later in 1993, with subsequent mass mortality.

Support of the hypothesis of delayed mortality of herring based on immunosuppression and infectious disease outbreak requires the following conditions, as discussed by Elston et al. (1997): (*i*) an appropriate level of oil exposure in 1989 that compromised the immune system without producing acute mortality, (*ii*) survival of the immunosuppressed herring for 4 years from the 1989 exposure until 1993, (*iii*) no exposure of the herring to opportunistic pathogens from 1989 to 1993, (*iv*) exposure of the herring population to a pathogen of sufficient virulence to cause mass mortality in late 1992 or early 1993, and (*v*) transmission of the virus not only to oil-exposed fish but to the unexposed fish as well.

This hypothesis also requires that the 1988 year-class (which were 1-year-old fish in 1989) be affected by the oil spill. Because the nondominant 1989 year-class was expected to represent only a small percentage of the spawning population, its hypothetical entire loss (which did not occur (Brown et

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al. 1994)) would have been insufficient alone to produce the magnitude of the 1993 decline. Similarly, the loss of the 1984 year-class would also have been insufficient to cause the 1993 decline. The 1984 year-class had dominated the biomass in 1989 but by 1992 had matured and faded, as expected. The 1988 year-class emerged as the major portion of the record biomass in 1992 (Fig. 3). To demonstrate a delayed effect, as posed under Hypothesis H3, one would have to explain how exposure conditions in 1989 induced an immunosuppressive effect in both exposed and unexposed fish that did not manifest itself until late 1992 or 1993.

Exposure necessary to compromise immunity

To our knowledge, the challenge tests that are necessary to experimentally demonstrate immunosuppression, in which the fish are exposed to petroleum hydrocarbons and then exposed to a pathogen, have not been done. However, two types of studies have suggested that impairment of fish immune systems can occur for a short time period following exposure to hydrocarbons.

The immune systems of fish from industrially contaminated water bodies were characterized by Robohm et al. (1979). They found higher mean levels of antibody in fish from polluted sites and later showed in laboratory experiments that although the primary antibody response in fish from polluted areas is elevated, the secondary response is depressed (Arkoosh et al. 1991; Robohm et al. 1993). Weeks and Warinner (1984) and Weeks et al. (1986) observed reduced macrophage migration and phagocytic activity in fish from a contaminated river, both of which returned to normal when the fish were held in clean water. Faisal et al. (1991) found that estuarine fish from five sites with sedimentary PAH concentrations from 1100 to 570 000 ppb had depressed proliferative responses by lymphocytes. However, holding in clean water produced recovery of this immune response marker within 4 weeks for fish from the least polluted sites and 20 weeks for fish from the most polluted site. Because the exposure history of fish in the wild is unknown, these studies do not contain the immunosuppression dose–response information that would indicate the environmental PAH levels of concern in terms of significant and (or) irreversible effects. Two of these studies indicated that an immunosuppressive response can be reversed shortly (within weeks) after exposure ceases. However, none of the studies addressed confounding factors, such as nutritional status, which can also affect immunity.

Also in laboratory exposure experiments, injection of benzo[*a*]pyrene or holding with PAH-contaminated sediments has produced impaired immune responses in fish based on in vitro measures of immune function (Payne and Fancey 1989; Faisal 1993; Arkoosh et al. 1994*a*, 1994*b*). A 4-month exposure of winter flounder (*Pleuronectes americanus*, previously *Pseudopleuronectes americanus*) to sediment contaminated with Venezuela crude oil produced decreased melanomacrophage centers above 25 000 ppb PAH and splenic atrophy above 200 000 ppb PAH (Payne and Fancey 1989). Increased macrophage aggregations were observed after the *Amoco Cadiz* oil spill (Haensly et al. 1982), and both increased and decreased macrophage aggregations have been observed in other fish from polluted areas (Wolke 1992). However, demonstration of a change in a morphological or biochemical marker thought to be a measure of immune function is not proof of immunosuppression (Arkoosh et al. 1994*a*, 1994*b*). Such proof requires tests of experimentally exposed fish challenged with a known pathogen. Thus, although Payne and Fancey (1989) interpreted their observations to indicate immunosuppression, they did not test organismic level response and did not provide reliable dose–response information. Similarly, although Arkoosh et al. (1994*a*, 1994*b*) reported that in challenge tests with a *Vibrio* pathogen, juvenile chinook salmon (*Oncorhynchus tshawytscha*) exposed to unknown environmental contaminants in the industrialized Duwamish Waterway had suppressed immune function and increased mortality, they could not provide dose–response information.

Although the above-cited studies indicate that PAH exposure can suppress fish immune systems, they indicate that exposure concentrations must be high, of the order of several thousand parts per billion, and present for weeks to months and that the effects, when produced, are rapidly reversed when PAH exposure is terminated. Thus, although the evidence indicates that immunosuppression under high, prolonged PAH exposure is possible for several fish species, the levels observed to induce immunosuppression discussed above are orders of magnitude higher than those observed in PWS during the spill. Therefore, to the extent that these other fish species model herring responses, the 1989 oil spill exposure was insufficient in concentration and duration to cause the immunosuppressive effect.

Survival of immunocompromised herring and exposure to opportunistic pathogens

A severely or long-term immunocompromised fish faces a gauntlet of environmental stressors and pathogens known to occur in herring, such as VHSV, viral erythrocytic necrosis (VEN), *Ichthyophonus*, *Eimeria*, and anisakid infections. As discussed by Elston et al. (1997), an immunosuppressed fish from the 1989 oil spill would not be expected to survive a 3-year exposure to these known pathogens and to other opportunistic microbes in the environment. If the immunosuppressive effect is mild and reversible, the experimental evidence is that compromised immune systems recover upon return to clean water (Weeks and Warinner 1984; Weeks et al. 1986; Faisal 1993). The condition that an immunocompromised population of fish would survive 3–4 years, only to succumb to a viral disease likely to be historically present in the population, is implausible.

The pathogenic VHSV has likely been historically present in herring but was just recently discovered (Meyers et al. 1994). Accordingly, herring potentially exposed to EVO in 1989 were likely exposed to VHSV before 1992–1993. Because VHSV has been isolated from herring from Kodiak Island, PWS, and southeast Alaska through British Columbia to Puget Sound (Meyers et al. 1994; Traxler and Kieser 1994), Meyers et al. (1994) concluded that Pacific herring could be a major reservoir of VHSV in the Pacific Northwest. Thus, it is highly likely that PWS herring were exposed to VHSV as well as to other pathogens before 1992–1993, and therefore, an epizootic would have been expected during or immediately after the spill if the PWS herring had been immunocompromised. Such an epizootic was not observed.

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Exposure to a virulent and transmissible pathogen

Present evidence suggests that VHSV is a pathogen with sufficient potency to contribute to herring mortality, but that mortality probably results when other factors interact with the virus. Tibbo and Graham (1963) described a Gulf of St. Lawrence case in which an epizootic affected stock levels. However, mass mortalities associated with VEN and VHSV infections have occurred in Pacific herring in southeast Alaska and British Columbia without leading to population-level effects. Meyers et al. (1986) described a mass mortality of herring that occurred in a semi-isolated bay in southeast Alaska and attributed that mortality to an epizootic caused by VEN, under conditions of stress on the local herring population from low salinity, crowding, and predator harassment. Kieser et al. (1995) reported the isolation of VHSV from several locations in British Columbia, Washington, and Alaska. In many instances, the virus was detected without any associated mortality or external lesions. Juvenile herring collected after a mortality incident in Prince Rupert showed VHSV in eight of 10 specimens. Kieser et al. (1995) concluded that it could not be determined whether the mortality and external lesions in Prince Rupert fish were derived from the virus or a from recent diesel fuel spill. These data support the possibility that viral pathogens are indigenous in Pacific herring over most of the Northeast Pacific Ocean and that the pathogens produce disease only when herring have been recently stressed by environmental conditions.

Because the advanced lesions observed in 1993 in PWS herring were sufficient to disrupt osmoregulation, Meyers et al. (1993, 1994) indicated that infection with VHSV could lead to mortality. However, they cautioned that VHSV has not been established as the cause of the 1993 decline of PWS herring. The observed histopathological features of VHSV infection in 1993 led Meyers et al. (1994) to conclude that VHSV was weakly pathogenic in herring. Thus, VHSV can most accurately be considered an opportunistic pathogen in herring that produces disease after the herring have been stressed by other factors, such as other infectious agents, spawning, capture, or nutritional deficiency (Meyers et al. 1994).

In summary, there is no direct evidence of immunosuppression in the PWS herring population before 1993 resulting from exposure to EVO. Although the available literature from laboratory studies suggests that high, prolonged PAH exposure can suppress portions of fish immune systems, the levels, duration, and nature of the laboratory exposures were substantially higher than those observed in the field during and after the spill. Further, there is a large gap in the time between potential exposure in 1989 and the events of 1993 and 1994. If a herring exposed in 1989 were immunosuppressed, it would likely not have survived the gauntlet of natural stressors and pathogens existing in the environment (Elston et al. 1997). Either we would have seen more sick fish or the population would have declined soon after the spill. Neither outcome has been observed (Fig. 3; Brown et al. 1994; Donaldson et al. 1993). Although immunosuppression of fish can occur in some instances, current knowledge of the mechanisms of immunosuppression and consequences for affected fish is incompatible with the observed data on PWS herring after 1989. The evidence is contrary to the hypothesis that a delayed effect of the 1989 oil spill caused the 1993 decline.

H4. Overfishing led to the decline of the PWS herring stock

Overfishing as the cause or major contributing factor in herring stock declines in other regions is well known (Myers et al. 1995; Hutchings 1996). For example, very large herring catches in British Columbia during the 1960's combined with several years of poor recruitment led to the collapse of the herring fishery and to its closure in 1968 (Schweigert 1995). Doubleday's (1985) analysis indicated that maintaining harvest rates at or near 20% of the spawning stock size prevents Pacific herring stocks from being exploited to the extent that they become vulnerable to collapse when the environment changes or poor recruitment occurs. Therefore, if overfishing were involved, an exploitation rate considerably above 20% would be expected in the years preceding the decline.

The exploitation rate of PWS herring has been within appropriate limits since the early 1980's. To prevent overfishing, ADFG established a sliding scale of harvest quotas up to 20% of the biomass in PWS (Funk 1994). Before 1994, the PWS herring fisheries would open when the biomass was above a threshold of 8400 t, and the quota would be 20% of the biomass when the biomass was above 42 500 t. In 1994, ADFG established a higher threshold for opening the fishery at 22 000 t. Funk and Sandone (1990) examined harvest rates from 1973 to 1988 and found that exploitation rates before 1978 were generally from 25 to 35% of the biomass, but that from 1979 to 1988, the harvest rates were at or below 20%. Before and after the spill, biomass was sufficiently high that PWS quotas were set at 20% of the biomass, and analysis indicated that the actual fishing rate when the fisheries were open was between 20 and 25% but definitely not as high as 40 or 50% of the biomass (F. Funk, ADFG, Commercial Fisheries Management and Development Division, 1255 W 8th Street, P.O. Box 25526, Juneau, AK 99802, U.S.A., personal communication). Thus, the observed harvest rates in PWS herring do not suggest that the PWS stock has been overfished (Donaldson et al. 1993).

Overfishing should lead to decreased biomass of the target species; in PWS, herring biomass has been increasing, as estimated by three techniques. In 1992, ADFG changed its technique for estimating the PWS herring spawning biomass from one based on peak aerial biomass determined from aerial surveys to one of biomass estimated from diver surveys of egg deposition. An ASA model (Funk and Sandone 1990; Funk 1993) also has been used to estimate herring biomass. Although the three techniques each yielded a different value, all concurred that the herring biomass levels in PWS in the 1990's were the highest since the 1970's (Funk 1993).

Further, independently collected age–weight–length information is not consistent with overfishing. If the PWS herring fishery were being overexploited, an increase in weight-at-age would be expected because there would be less competition for available food resources. However, the weight-at-age of PWS herring has fallen since the mid- to late 1980's (Bailey et al. 1995), suggesting instead a density-independent decrease in food supply or density-dependent response, in

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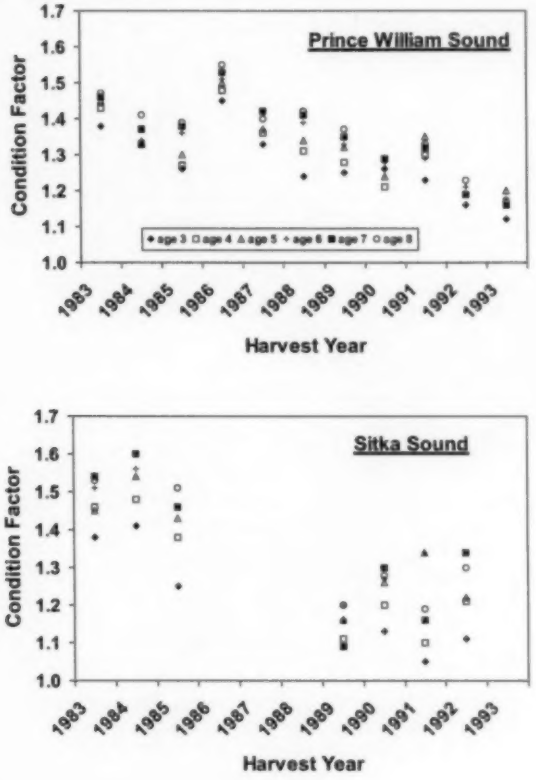
Fig. 8. Condition factors of Pacific herring in PWS and Sitka Sound, 1983–1993.



which growth slows under increasing biomass due to higher competition for food.

In summary, the ADFG harvest data do not indicate that the PWS herring population was overfished, and supplemental fisheries data are not consistent with an overfishing hypothesis.

H5. Underfishing allowed the herring biomass to increase to the point that density-dependent mechanisms led to the decline

Hypothesis H5 follows from the suggestion by Brown et al. (1994) that the 1989 oil spill related closure of the fishery resulted in underfishing that could have further enhanced a density-dependent response and contributed to the 1993 decline. The 1989 closure did cause about 18% of the biomass to go unharvested (Pearson et al. 1995). To support this hypothesis, the unharvested biomass would have to have been sufficient to bring the PWS population over the carrying capacity of its environment and to thereby cause the decline.

Although there are no direct measures of the PWS carrying capacity for herring, there is some evidence that the PWS herring population may have been approaching the carrying capacity in the pre- and post-spill years. The annual PWS herring biomass has increased since the early to mid-1980's (Fig. 1), and since 1987, herring condition factor (Fig. 8) and weight-at-age have been falling.

The timing of the decline and the observed age-class distributions of the PWS herring population argue against the underfishing hypothesis. The dominant 1984 year-class contributed to the above-average biomass in 1990 and then began to wane, as expected (Fig. 3). If the direct effect of the 18% unharvested biomass were to raise the PWS population above some threshold of carrying capacity, the decline would have been expected in 1990, when the 1984 year-class still dominated the population and the effect of the additional biomass was at its maximum. However, the decline occurred in 1993, when the 1984 year-class had faded and the 1988 year-class had recruited strongly.

To produce a decline in 1993, the underfishing hypothesis requires an indirect effect on the 1988 year-class. Because the 1988 year-class consisted of juveniles not subject to fishing in 1989, the closure did not change the numbers or biomass of the 1988 year-class. Subsequently, the 1988 year-class recruited strongly in 1991 and was dominant before and during the 1993 decline. The fact that between 1991 and 1992, the 1988 year-class produced one of the strongest recruiting year-classes in PWS history is contrary to any competitive effect that may have resulted from the 18% increase in adult biomass in 1989. If anything, increasing the adult biomass would be expected to depress the juvenile biomass through food competition.

Therefore, underfishing in 1989 or in postspill years 1990–1992 does not appear to be a major cause of the 1993 decline; however, the possibility that underfishing contributed to the 1993 decline cannot be completely dismissed. A direct effect from underfishing is not consistent with the timing of the decline or with the observed age-class distributions in PWS, and an underfishing hypothesis would have to provide for an indirect competitive effect on the strongly recruited 1988 year-class that is contrary to what actually occurred.

H6. Poor nutrition alone or in conjunction with a disease caused by an opportunistic pathogen produced substantially lower herring survival that then caused the decline

A classic explanation of population collapse is that of an abrupt decline when the population exceeds the carrying capacity of its environment (Odum 1993). This set of hypotheses posits either that the PWS biomass has increased beyond the carrying capacity, producing a density-dependent response (Hypothesis H6*a*), or that the carrying capacity of the PWS environment has fallen, producing a density-independent response (Hypotheses H6*b* and H6*c*). Both types of response can occur at the same time. All the variant hypotheses require that poor nutrition occur in the PWS herring through some sort of mismatch between the PWS herring population level and its food supply. After discussing the evidence for biomass increases, food supply shifts, and poor nutrition for each variant hypotheses, we consider whether poor nutrition alone or in conjunction with an infectious disease was sufficient to produce the decline.

H6a. Recently increasing herring biomass increased intraspecific competition for prey

This hypothesis posits that the herring biomass in PWS reached a level sufficiently high to cause poor nutrition that

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Fig. 9. Average weight change for Pacific herring in PWS from fall to spring, 1984–1994.

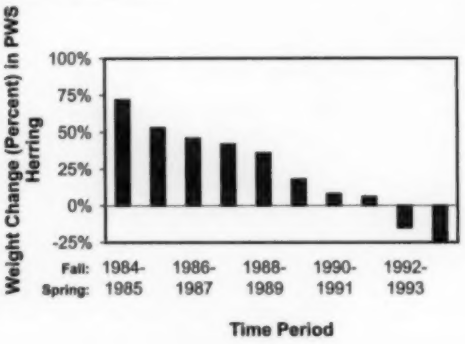
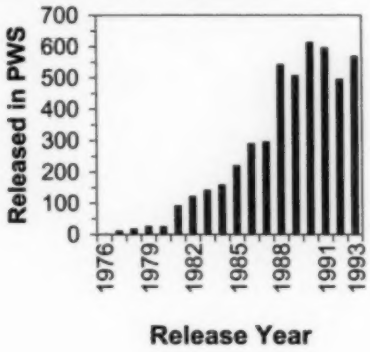


Fig. 10. Pink salmon fry releases into PWS.



in turn decreased survival either alone or in conjunction with disease. Under this hypothesis, PWS herring biomass would be expected to reach high levels, and poor nutrition would be evident at the high biomass levels.

Since the early 1970's, when the PWS sac-roe herring fisheries began, herring fishery harvests and herring biomass within PWS have been generally increasing (Figs. 1 and 2). The ASA modeling of Funk (1993) has shown that the highest biomass levels in PWS have been seen since 1988, when the strong 1984 and 1988 year-classes recruited to the spawning population (Fig. 3).

The increasing PWS biomasses have been accompanied by changes in several measures of PWS herring growth and condition. Since the early to mid-1980's, the condition factor (Fig. 8) has been decreasing, and since 1986 or 1987, weight-at-age has been falling (Brown et al. 1994; Funk 1994; Bailey et al. 1995). Similar patterns of changes in biomass, condition factor, and weight-at-age can be seen for Pacific herring in Sitka Sound (Fig. 8). However, the changes at Sitka were not as dramatic and were not accompanied by a large population decrease.

Other evidence of poor growth in PWS herring includes decreases in the fall to spring weight gain. Generally, weight-at-age increases in PWS herring from the fall to the spring (Fig. 9). However, beginning in 1985, the magnitude of the weight gain was decreasing to the point that in 1993 and 1994, actual weight loss occurred between the fall and spring fisheries, and length did not increase (Fig. 9). Therefore, the available data do not disprove the hypothesis of an increasing herring biomass and increased competition for prey.

H6b. Recently increasing biomass of other fish increased interspecific competition for prey

This hypothesis posits that not only have increases in herring biomass heightened intraspecific competition for prey, but increased abundance of other species preying on the same food has heightened interspecific competition for food.

Although systematic direct measurement of PWS zooplankton abundance is not available in a long time series, the limited zooplankton data indicate lower zooplankton abundance in recent years. Since 1981, the PWS Aquaculture Cooperation has been measuring zooplankton abundance at selected locations in PWS in the spring to determine the optimal timing for release of salmon fry from the PWS hatcheries. With the exception of 1 year of high zooplankton volume (1989), spring zooplankton abundance in PWS has been below average since 1986 (Fig. 7). A more detailed presentation of the 1992 and 1993 zooplankton volume data for Erlington Passage in PWS by Bailey et al. (1995) showed that the zooplankton volume in 1992 and 1993 was anomalously low compared with the long-term mean.

As PWS zooplankton abundance has fallen, the number of pink salmon (*Oncorhynchus gorbuscha*) fry released into PWS has risen exponentially from 1977 through 1988 (Fig. 10). In 1986, almost 300 million salmon fry were released; in 1988 and thereafter, over 500 million salmon fry have been released annually. It is not clear whether lower zooplankton levels in recent years result from cropping by the large numbers of released fry or from some another cause. However, because salmon fry, as well as juvenile and adult herring, feed on mature copepods, large releases of salmon fry and increasing herring biomass raise valid concerns that food competition could be increasing, thereby limiting food availability. Since 1981, the condition factor in the fall PWS herring bait fishery was highest for 1985 and 1989, the years with above-average zooplankton abundance (Fig. 7). This observation is consistent with the concept that herring growth in PWS is likely governed in part by zooplankton abundance. These data cannot exclude the hypothesis of a potential effect on herring from interspecific competition for prey.

H6c. Large-scale oceanic processes reduced food supply that in turn lowered the nutritional status of the PWS herring

Decreases in food supply from large-scale oceanic processes are a potential hypothesis to explain the 1993 PWS herring decline. Other areas of the Pacific Ocean are showing major fish and bird population declines, resulting from food supply declines, caused in turn by regional changes in ocean climate (Brodeur and Ware 1992; Bigler and Helle 1994; Lenarz et al. 1995; Roemmich and McGowan 1995). An abrupt decrease in food supply when the herring biomass is at record-high levels would be expected to have a substantial effect on population levels.

Large-scale changes in food supply of the North Pacific Ocean during recent years have been suggested by a number of studies (Muter et al. 1992). The analysis of Beamish and Bouillon (1993) found that the long-term trends in the an-

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nual catches of three salmon species by Canada, Japan, Russia, and the United States were parallel and indicated that common events in the ocean climate over the whole of the North Pacific Ocean had affected salmon production. Declines in salmon catches were related to sharp decreases in the Aleutian Low Pressure index (ALPI). Declines in the ALPI indicate high pressure or weak lows over the North Pacific Ocean. In the mid-1980's, the ALPI reached the highest point in the time series since measurements began in 1899 and subsequently began to weaken. Beamish and Bouillon (1993) found a significant positive correlation between the ALPI and food resources measured as copepod abundance and suggested that a large increase in copepod abundance starting in 1976 was associated with more intense Aleutian Lows. The evidence of lower growth hypothesized by Beamish and Bouillon (1993) was subsequently observed by Bigler and Helle (1994), who noted decreases in average body size on an ocean-wide basis in five species of Pacific salmon from 1975 to 1993.

Bailey et al. (1995) also found major changes in the GOA ecosystem since 1977 and suggested that the El Niño – Southern Oscillation (ENSO) could be involved. In winter 1992, the 1991–1993 ENSO led to sea level pulses and anomalous circulation patterns in the GOA. Bailey et al. (1995) reported that although ENSO events may favor recruitment of some groundfish and be adverse to recruitment of herring and other small pelagic fish, the effects on fisheries of ENSO events are not consistent. They also concluded from the inconsistent nature of ENSO effects on GOA commercial fish that ENSO events are more likely to affect commercial fish species through initiating major shifts in the ocean climate than through specific or direct effects on fish populations and recruitment.

Nutrition and disease

Although poor nutrition alone could have caused the 1993 decline, the pattern of survival rates and the observation of disease argue that poor nutrition and disease acted together. The population decrease from 1992 to 1993 was equivalent to a shift in survival from its normal value of 68% to 34% (Brown et al. 1994). Because the age structure of PWS herring shows no unusual shifts between 1992 and 1994, the conditions causing the 1993 decline must have affected all the year-classes equally (Brown et al. 1994).

Several measures discussed above indicate that the nutritional status of PWS herring population has been declining since before the spill, and coincident with the weight loss from fall 1992 to spring 1993 was the observation of VHSV in PWS herring during spring 1993 and the documentation of other infectious diseases in the population in 1994 (Elston et al. 1997; Marty et al. 1998). VHSV is an opportunistic pathogen that produces disease when the host has been stressed by other factors, one of which is poor nutrition (Meyers et al. 1994). However, it has not been established whether the VHSV outbreak caused mass mortality sufficient to produce the magnitude of the 1993 decline (Meyers et al. 1994). Infections caused by other diseases, most notably the fungus *Ichthyophonus hoferi*, were documented from PWS herring populations between 1989 and 1994 (Elston et al. 1997; Marty et al. 1998). *Ichthyophonus* prevalence was estimated at between 16 and 29% in 1994, depending on the population examined. Marty et al. (1998) reported that the 1994 prevalence of this disease was more than double that measured in PWS herring in the years since 1989. The disease results in significant lesions linked to morbidity and mortality and appears to progress rapidly once adult fish are on spawning grounds and under stressful conditions (Elston et al. 1997). Thus, like VHS, infection with *Ichthyophonus* may at times be an important factor, but it appears to act in a secondary fashion to accentuate the effects of other stresses on the population.

In summary, the data cited in the previous section indicate both increasingly higher herring biomass in PWS leading up to the decline and increasingly lower weight-at-age and lower condition factors in PWS herring. Long-term trend data show that zooplankton biomass has been below average for several years and that the condition factor of herring was decreasing consistently from 1984 to 1991 to the point where overwintering fish actually lost weight in 1992 and 1993. These data are consistent with a density-dependent mismatch between PWS herring population levels and food supply. Therefore, we cannot reject the hypothesis that poor nutrition alone or in combination with disease produced the herring population decline in 1992–1993.

H7. Disease caused the 1993 decline

This hypothesis posits that disease was sufficient by itself to cause the decline and requires the disease agent to be highly virulent. Some sort of triggering mechanism would be expected.

H7a. Disease alone caused the 1993 decline

As discussed under Hypothesis H3, VHSV and *Ichthyophonus* are pathogens with sufficient potency to contribute to herring mortality, and this hypothesis posits that either pathogen is sufficiently virulent to cause mass mortality by itself. However, from the observed histopathological features of the 1993 VHSV infection, Meyers et al. (1994) concluded that VHSV was weakly pathogenic in herring. For Pacific herring, Meyers et al. (1994) considered VHSV to be an opportunistic pathogen that produces disease after the herring have been stressed by other factors. Therefore, Meyers et al. (1993, 1994) cautioned that VHSV has not been established as the cause of the 1993 decline of PWS herring. Similarly, *I. hoferi* also appears to be an opportunistic pathogen whose prevalence increases when herring are stressed by other factors. Thus, although disease probably had a key role in the 1993 decline, it is unlikely that it is the sole agent causing the decline.

H7b. Low temperatures triggered a disease outbreak that in turn reduced survival

Hypothesis H7*b* posits that a cold snap triggered the disease outbreak that caused the PWS herring decline. European fish farmers have found that VHSV outbreaks and high mortalities in trout occur during winter cold snaps (Conroy and Herman 1970; Roberts and Shepherd 1974). The experiments of Castric and De Kinkelin (1984) showed that in sea bass (*Dicentrarchus labrax*) and turbot (*Scophthalmus maximus*) infected with VHSV, disease occurred only at temperatures below 15°C. Similarly, *Ichthyophonus* disease appears

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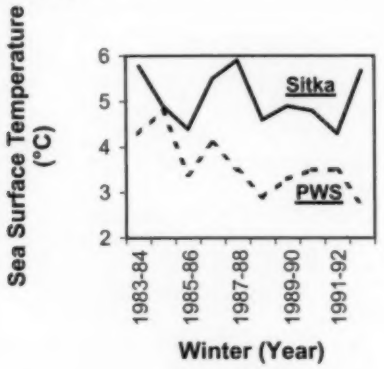
Fig. 11. Coldest average monthly sea surface temperature in PWS and off Sitka, Alaska.



to be triggered by lower water temperatures, at least in Atlantic herring (Wolke 1975).

Although the sea surface temperature data are too limited and too coarse to support definitive statements, NOAA monitoring data for stations off Montague Island show some evidence for cold temperatures in PWS during winter 1992–1993 compared with the Sitka area for the same time period (Fig. 11). Additional data from a monitoring buoy deployed north of Naked Island since June 1992 showed that sea surface temperatures were very cold, about 4°C in December 1992. Unfortunately, there are no January or February data because the buoy was recovered for maintenance. Bailey et al. (1995) reported anomalous GOA circulation in winter 1992 that could have prevented warmer GOA surface water from entering PWS. Thus, although data indicate a cold winter period, there is insufficient evidence to affirm or deny that a cold snap could have triggered either an VHSV outbreak in 1993 or an *Ichthyophonus* outbreak.

H8. Increased predation reduced the population level

Predation plays a major role in determining the abundance of herring off the coast of British Columbia (Schweigert 1995). Unfortunately, the data on herring predators in the GOA and PWS are limited, fragmented in duration, and spotty in terms of the species considered. Further, not all potential predators or interactions are known or studied. Despite these caveats, the arrowtooth flounder (*Atheresthes stomias*), which is known to use herring as a major prey item, has increased in abundance the GOA in recent years (Livingston 1995). Recent studies (Walters et al. 1986; Purcell and Grover 1990; Tanasichuk et al. 1991) suggested that herring predators, such as squid (*Loligo opalescens*), jellyfish (*Aequorea victoria*), Pacific cod (*Gadus macrocephalus*), and walleye pollock (*Theragra chalcogramma*), could be more important than heretofore imagined; however, we have no comparable data on such species for the times before 1993.

Despite the lack of information, we argue that increased predation does not seem to be more than a potential contributing factor in this population decline. However, after the long-term downward trend in condition and growth observed for the PWS herring, weakened condition could lead to increased vulnerability to predation (Bailey et al. 1995). Also, if food supply were limited in general, prey switching could lead to increased predation on herring. For pelagic predatory species, changes in water temperatures can lead to increased metabolic costs at the same time that food supply could be changing. However, because of the lack of information, the hypothesis that increased predation contributed to the 1993 decline must remain for the present as neither discounted nor affirmed.

H9. Natural chaotic population dynamics produced a large, abrupt change in the PWS herring population

Steele and Henderson (1984) noted that abrupt and dramatic population fluctuations in pelagic fish stocks, including herring, occur without a clear, obvious, or simple relationship to variations in the physical or biological ocean environment. Moreover, the abrupt changes in stock levels are not always associated with abrupt or large changes in physical or biological factors. Using data from North Sea herring stocks, Steele and Henderson (1984) developed a simple population model with multiple equilibria under stochastic variability that showed the observed behavior. For several carrying capacities and predation rates, the model had several solutions. The authors concluded that small changes in the physical or biological environment can produce large, abrupt changes in fish stocks. A longer time series on the variation in the PWS herring stock is needed to fully test this hypothesis and to assess whether the events of 1993 and 1994 represent a domain shift in the dynamics of the PWS ecosystem and fisheries.

Conclusions

Based on our review of the data and analyses of alternative hypothesis, we are convinced that the combination of increasing PWS herring biomass and decreasing food supply led to poor condition of PWS herring, which resulted in the 1993 population decline (Table 4). The long-term downward trend in herring condition and size-at-age is well established by directly measured data and is consistent with the long-term trend toward lower size-at-age in several salmon species along the Pacific Coast of North America (Bigler and Helle 1994). We found evidence that other natural causes could have contributed to the decline, but without more specific data, we cannot establish the degree to which disease, cold water temperatures, increased predation, or other natural factors also negatively affected the herring population. We acknowledge that stochastic events in the dynamics of the PWS ecosystem and herring population could explain the decline, but a longer time series on the PWS herring stock is needed to assess this explanation. We did not find evidence to support the hypotheses that the effects of overharvesting, underharvesting, or the 1989 oil spill were responsible for the 1993 herring fisheries collapse. Measured levels of PAH following the oil spill in the water column were well below levels known to be toxic to herring, and the vast majority (over 90%) of spawning in 1989 and 1990 occurred outside the oil spill impact area. Therefore, we conclude that poor nutritional status, either alone or in combination with disease, is the most likely explanation of the 1993 decline.

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Table 4. Summary of hypotheses tested to explain the 1993 collapse of the Pacific herring population in PWS.

Hypotheses for PWS herring decline in 1993	Findings and status	Conclusion
Oil spill		
H1. Acute effects in 1989	Insufficient exposure and no toxic effects on population	Reject
H2. Toxic effects of lingering oil after 1989		
H2*a*. Direct effect lingering oil	Low exposures and no reported effects	Reject
H2*b*. Indirect effect on food supply	Record-high levels of zooplankton during oil spill	Reject
H3. Delayed effects	No evidence of delayed immunosuppression; mechanism implausible	Reject
Harvesting effects		
H4. Overfishing	Harvest statistics were within guidelines; not consistent with age–weight–length data	Reject
H5. Underfishing	Not consistent with timing of the decline or with observed year-class distribution	Reject
Natural factors		
H6. Poor nutrition and disease		
H6*a*. Intraspecific density-dependent response	Increasing herring biomass and decreasing weight-at-age since 1985	Most likely
H6*b*. Interspecific competition	Increasing releases of salmon fry from hatcheries	Possible
H6*c*. Oceanic/meteorological processes	Large-scale changes in ocean climate of North Pacific region	Partial
H7. Disease		
H7*a*. Disease alone	Histopathology does not indicate sufficient virulence to pathogen alone	Partial[a]
H7*b*. Low temperature and disease	Some low temperatures and anomalous circulation, but temperature records incomplete	Inconclusive
H8. Increased predation	Incomplete records of predator abundance	Possible
H9. Natural chaotic population dynamics	Environmental changes difficult to measure	Possible

[a]Not likely alone; likely with poor nutrition.

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